THE
AMERICAN NATURALIST

VOL. LVII. *January–February, 1923* No. 648

A NOTE ON SYMMETRY AS A FACTOR IN THE EVOLUTION OF PLANTS AND ANIMALS

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REPORTING AN ILLUSTRATIVE STUDY OF THE TRANSFORMATION OF THE AORTIC ARCHES IN THE SHEEP BY DR. GEORGE H. JACKSON, JR.

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THE pretentiousness of this subject, even when qualified as a note, is greatly at variance with the simple nature of the observations to be presented. But simple and familiar as they are, they seem to be of considerable significance, and for the author, at least, have been of perennial interest.

Symmetry is here to be considered in the wide and non-mathematical sense of a balanced and harmonious relation of parts or organs, and as displayed in three main types—bilateral, radial, and spiral symmetry. In bilateral symmetry, which is the simplest form, the laws are, according to Bichat, that whenever an organ is beyond the median line it should be double; it should be simple, on the contrary, but regular, when it falls upon it.[1] Fixing his attention upon this one form of symmetry, so conspicuous in the disposition of the limbs in animals, and contrasting it with what seemed to him the wholly disorderly arrangement of limbs in trees, Bichat declared that in forming the plant "nature, one might say, has

[1] Bichat, Xav., "Mémoire sur les rapports qui existent entre les organes à forme symétrique, et ceux à forme irrégulière," *Mém. de la Soc. Méd. d'Émulation*, Paris, An VII (1798–9), T. 2, p. 482.

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forgotten her rule and compass." Radial symmetry, so prevalent in plants, but abundantly associated with both the other types, is a more complicated or higher form than the bilateral. For symmetry, as Jaeger has said, is a term to draw attention to a certain process of repetition manifest in a figure, its symmetry consisting in the regular repetition of its definite parts, so that by superimposing or otherwise, these parts may be made to coincide.[2] This principle he illustrates with a reference to the surprising and very beautiful symmetrical effects obtained in mirror-kaleidoscopes, due to the repeated reflection in regularly arranged little mirrors, of a number of insignificant pieces of glass thrown together by mere chance. In black and white he shows the same thing by a random scattering of dots in a wedge-shaped area, which needs only to be repeated in rotation, making this wedge the segment of a regular polygon, to produce a complex symmetrical pattern. "The splendor and fascinating beauty of a great number of living creatures," he declares, "are in each case caused by the mere action of symmetrical *repetition.*" Since in bilateral symmetry there is but a single repetition, it may be regarded as simpler than the radial, which requires two or more.

In the radial arrangements of both animals and plants there is a certain preference for the pentamerous or pentagonal form, "which is the more remarkable," Jaeger comments (p. 61), "since this particular symmetry is quite impossible for crystalline matter." Thompson notes that Kepler in 1611 was seeking "an explanation of the mysterious and even mystical beauty of the five-petaled flower,"[3] and both Jaeger and Thompson review the extensive subsequent literature bearing upon its mathematical interpretation—a problem "not to be set and answered in a word."

The pentamerous whorl of plants is often clearly a condensed spiral, and spiral arrangements, so strikingly

[2] Jaeger, F. M., "Lectures on the Principle of Symmetry," 2d ed., Amsterdam, 1920, pp. 2–4.

[3] Thompson, D'A. W., "On Growth and Form," Cambridge, 1917, p. 480.

evident in the higher plants, are apparently more frequent in the viscera of the higher animals than is generally recognized. They may involve no repetition of parts, and then are a form of symmetry only in so far as they are an orderly and geometrical disposition of organs.

Symmetry in organisms is presumably the result of various tensions, diffusions, effects of gravity and other physical causes, with which the present morphological study is not at all concerned. Symmetrical arrangements may proceed from an even distribution or dispersal of blood or sap, which in turn they would favor, being thus serviceable arrangements; and they are often held to be expressions of equilibrium, mechanical stability and repose. But in organisms they seem difficult to maintain, so that departures from a symmetrical plan are frequent. If a new symmetrical relation is reached, or an approximation thereto, a new form may be produced of greater or less permanence. From the preponderance of symmetrical forms in nature, it may be assumed that there is a special tendency to produce them; and unsymmetrical arrangements, being relatively exceptional and apparently more variable, are perhaps transient, and destined to be replaced by new ones, more symmetrical and enduring. If this be true, a great range of future changes in the anatomy of plants and animals seems possible, some of which one might venture to predict. An instance will be cited where symmetry is so nearly attained that, due to superficial examination, it has been assumed already to exist. In other cases departures from primitive symmetry have been such that no symmetrical rearrangement seems ever possible. With such suppositions in mind it is proposed to examine two instances in which the factor of symmetry may be of controlling importance—first, in what seems the simpler matter, the floral variations in the genus Campanula; and then in a more complex problem in mammalian embryology.

FLORAL VARIATIONS IN CAMPANULA

Campanula is a well-marked genus of more than a hundred species, several being very common in cultivation, growing chiefly in the temperate regions of the northern hemisphere. The Alps, Italy, Greece, the Caucasus and the Altai Mountains are, in De Candolle's expression, their native land, and in whatever direction one leaves it, the number of species promptly diminishes. Their flowers, in the symmetry of which alone we are interested, have normally a five-cleft calyx which is adherent to the ovary, a five-lobed bell-shaped corolla, five stamens, and either three or five stigmas associated with a corresponding number of carpels. The species with three carpels greatly predominate, outnumbering those with five by approximately ten to one.[4] It is hardly possible to know which of these arrangements is primary and gave rise to the other—the somewhat unsymmetrical form which is prevalent, or the less usual, perfectly symmetrical flower with all its parts in fives. The latter will be presented first, merely for convenience of description. Against regarding such flowers as primitive, Eichler has written the following vigorous protest ("Blüthendiagramme," Leipzig, 1875, Th. 1, p. 9):

> An example of unacquired heteromery, very frequent especially among dicotyledons, consists in this, that the pistil has fewer members than the preceding whorls—that it is "oligomerous." It has been attempted time and again to explain this by abortion from isomery (see, *e.g.*, A. Braun, "Verjüngung," p. 105; Wydler, in several places) yet in most cases there is no ground for such an assumption. Actual evidence is wholly lacking. One sees, for example, in the otherwise 5-merous flowers of the Apocynaceæ, Solanaceæ, etc., from the first no more than two carpels—of abortive ones, no trace—and placed in such position opposite each other that the theory making them the only two members to develop out of an original 5-merous cycle is clearly unjustified. That now and then a 3-, 4-, or 5-merous cycle actually appears, shows nothing more than that the number of carpels can vary, just as happens in the other

[4] De Candolle, in his "Monographie des Campanulées," Paris, 1830, recognized 13 species with 5-locular capsules and 5 stigmas, and 124 species with 3-locular capsules.

whorls. Why under these circumstances one should insist on isomery is not to be understood. Were *all* the whorls of the same number, there would be some ground for the assumption; but when the leaf-arrangement at the base of the shoot usually begins with a lower divergence (the two bracts, placed at ½) there can be nothing strange in the idea that at the apex there is a falling back to a similar divergence.

A modification of Eichler's "floral diagram, or ideal section" of *Campanula medium,* a completely symmetrical form with five carpels, is shown in Fig. 1 *A*. In this species, where the sepals meet in the outer circle, there are certain appendages, shown in the diagram as loops. The petals alternate with the sepals, and the stamens with the petals. But the carpels or cells of the ovary are opposite, and not alternate with the stamens. In the midst of each carpel is seen the section of its *carinal vein* (or nerve), which in the actual flower extends upward as the midrib of the adherent sepal.

The unexpected failure of the carpels to alternate with the stamens has its explanations. After Brown had announced his opinion that the typical flower possessed two alternating rings of stamens, being "diplostemonous," De Candolle applied a similar idea to the interpretation of this campanula. He assumed that a cycle of alternating floral structures once existing between the present ring of stamens and the carpels had been suppressed, thus leaving the carpels opposite the stamens. But when he found that in two other species of what Linnæus considered Campanula, the arrangement of parts was precisely as in *C. medium* except that the carpels did alternate with the stamens, the hypothesis became somewhat involved. In these species the stamens stand opposite the ovarian septa, and thus they alternate with the carinal veins. Dumortier had already made the new genus Musschia for one of these species, and De Candolle proposed Platycodon for the other. But the explanation remains unsatisfactory, for as Penzig recently points out, among all the near allies of the Campanulaceæ there is actually no case of diplostemony; and Eichler, after

considerable discussion, concludes curtly,—"The fact is, we have two sorts of carpel-orientation in the Campanulaceæ; how it is explained, the future may show, but the interpretations proposed hitherto are untenable" (*l. c.*, p. 296). A further suggestion as to its significance will be found in the following paragraphs.

In *C. medium* numerical variations of the sort which occur so freely in species with three carpels have not been as often or so carefully reported. Either they are less common because of the greater stability of the completely pentamerous flower, or the other more conspicuous abnormalities of this species have caused them to be overlooked. For *C. medium,* according to Heckel, has "become classic through the facility with which it produces double flowers formed of gamopetalous corollas enclosed one within the other," and alternating regularly. The calyx is often petaloid, and may be multiple; Heckel reported a terminal flower with three calyces and four corollas, but with normal androecium.[5] Fasciation of the stem is frequent, and of similar origin are the fused flowers with increased numbers of parts; but such monstrous forms belong in a different category from the numerical variations under consideration. In the Botanical Garden at Modena, Penzig saw a plant in which all the flowers were transformed into leafy shoots. On the elongated floral axis were many lanceolate leaves spirally arranged, and only at the tip there stood a whorl of three normal carpels with long stigmas.[6] Possibly this is a reversion to the primary number of carpels for the genus. In otherwise normal flowers of *C. medium,* the number of carpels may be reduced to four, or "accidentellement" to three, as stated by De Candolle, who thought that he had figured such a specimen, but it does not appear in his plates. Instead, we find a section of a 4-celled ovary here reproduced as Fig. 1 *f*. Its asymmetry is manifest

[5] Heckel, E., "Nouvelles monstruosités vegetales," *Bull. de la Soc. Bot. de France,* 1882, T. 29, p. 308–309.

[6] Penzig, O., "Pflanzen-Teratologie," 2te Aufl., Bd. 2, 1921, p. 534.

in the distribution of the carinal veins, one cell having two veins in its wall, but the others only one.

Before considering the variations in species with 3-celled ovaries, it may be noted that a 4-parted whorl forms a particularly disharmonious combination with one of five parts, whereas the association of 3-parted and 5-parted whorls more nearly approaches symmetry. The relations in these two combinations are shown in the diagrams Fig. 1 *D* and *E*, in which a circle of five anthers (such as might be sectioned in a campanula-bud) is shown in relation with 4-celled and 3-celled ovaries, respectively. The combination in Fig. 1 *D*, with a 5-parted corolla and calyx added, is not common in normal plants, but it occurs in Symphoricarpos and Parnassia, and is tolerated. Parnassia is said to have three and five carpels as variants, and the genera allied to Symphoricarpos have two, three, or five. The combination shown in Fig. 1 *E*, on the contrary, is very common. This is clearly associated with the fact that its whorls, showing respectively the 1/3 and 2/5 arrangements, are successive stages in the phyllotactic series, moving toward the "ideal angular divergence"; but the 1/4 arrangement of the carpels, as in Fig. 1 *D*, finds no place in that series. With the establishment of a 4-carpellate gynœcium, the loss of the fifth stamen, petal and sepal may be anticipated, producing a tetramerous flower with alternating whorls, the members in each cycle adjusting themselves to an angular divergence of 90°.

The parts in a tricarpellate campanula are placed normally as in the diagram Fig. 1 *B*. If a pentamerous flower is lateral and extends horizontally from the stem, the whorls of sepals and petals are usually so oriented that a sepal is directed upward, and a petal downward, in the midline.[7] The flower-stalk has two bracts, one on each side, which ordinarily lie in a horizontal line. In *C. rapunculoides* these bracts are sometimes nearly vertical, and a median sepal may be below instead of above. Eich-

[7] Brown, Robert, "Observations, etc., 1826," in Misc. Bot. Works, Ray Soc., 1866, Vol. 1, p. 291.

ler found that in the Campanulaceæ generally, a sepal, genetically the second one, is uppermost. He observed the reversed position "only exceptionally, yet not exactly rarely." "I found it especially frequent in Specularia, but it is nowhere normal; and if Hofmeister plainly states that the odd sepal in *C. medium* is median and

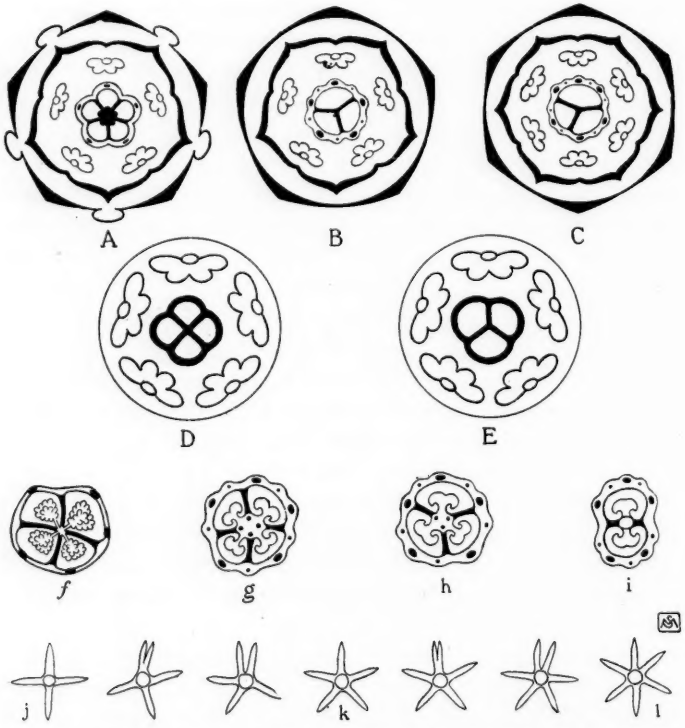

FIG. 1. *A*, diagram of the symmetrical flower of *Campanula medium* L. (modified from Eichler). *B*, diagram of the asymmetrical tricarpellate *C. rapunculoides* L. *C*, diagram of the nearly symmetrical tricarpellate hexamerous variant of *C. rapunculoides* L. *D* and *E*, diagrams of possible relations of the 4- and 3-carpellate ovary respectively to the 5-merous cycle of stamens. *f–i*, sections of ovaries showing the relation of the septa to the carinal and sutural veins: *f*, a 4-carpellate variant of *C. medium*, with carinal veins only (after De Candolle); *g*, *h*, and *i*, 4-, 3-, and 2-carpellate forms of *C. rapunculoides*. *j–l*, calyx-patterns of *C. rapunculoides*, varying from the normal (*k*) to the 4-merous form (*j*), and to the 6-merous form (*l*). (Except as otherwise stated all figures are from the author's sketches carefully redrawn by Mr. F. Schuyler Mathews.)

below, then I must contradict it."[8] Another variable feature is the orientation of the three carpels. Eichler finds that "ordinarily the odd carpel is upward (as in Fig. 1 *B*), but sometimes the reversed position occurs (Fig. 1 *E*)." In the allied genus Phyteuma, Wydler likewise found the unpaired carpel upward, or toward the main stem, "most frequently,—less often, median and below."[9] As shown in Fig. 1 *B*, the carpels may be of unequal size and not accurately oriented. The distribution of the veins in their outer walls is highly unsymmetrical. There are ten of these veins,—five carinal, which are continued as midribs of the sepals, and five, usually somewhat smaller, sutural veins (so designated by De Candolle), midway between the sepals and in line with the midribs of the petals. Since some of these veins arise as branches of the others in the lower portion of the ovary, it is only near the top that they become evenly spaced. Ordinarily one of the three carpels includes two carinal and two sutural veins; another has one carinal and two sutural; and the third has two carinal and one sutural. This distribution of veins is shown in *C. rapunculoides* (Fig. 1 *B*) and in a section from *C. rotundifolia* figured by De Candolle, and its marked asymmetry may well be correlated with the abundance of variations in these and allied species.

The asymmetry of the trimerous pistil is further emphasized by the arrangement of the hairs which beset the upper part of its style in ten longitudinal ranks. These ten rows of collecting hairs are evidently due, as De Candolle observed (*l. c.*, p. 18–21), to the close approximation, in the bud, of the five anthers to each other and to the style, around which they form a closed ring. As suggested in Fig. 1 *E*, the notches between adjacent anthers together with those in the midst of each anther form ten longitudinal grooves which offer the only available space into which the hairs may grow out.

Writers on monstrosities have found little of interest in the minor numerical variations of the tricarpellate campanulas, usually referring to them as "well known" when describing some great thing like a flower with 10,

[8] Eichler, A. W., "Blüthendiagramme," Theil 1, Leipzig, 1875, p. 294.
[9] Wydler, H., "Kleinere Beiträge," Flora, 1860, Jahrg. 43, p. 594.

13, or even 30 petals. But Witte placed on record 22 different numerical combinations which he observed in *C. rotundifolia* growing in northern Sweden; and Dahlgren, also in Sweden, found in four species, 58 different combinations.[10] He records 7 others seen by Witte and Sylvén, of which he failed to find examples, and believes the list still incomplete; it includes no flower with as many as ten parts in any whorl. The special value of Dahlgren's tabulation is that it gives the number of examples which he saw of each form, though the thousands of normal flowers among which they occurred were not counted. Of *C. rapunculoides* he examined relatively few plants and found only 20 numerically abnormal flowers; of *C. rotundifolia* he has 277 variants, of *C. persicifolia,* 122; and of *C. patula,* 420—altogether 839 numerically abnormal flowers. These variations are summarized in Table I. The figures in each column indicate the number of instances the whorl named at the left contained the number of parts placed at the head of the column; that is, 9 flowers among the 839 variants had 3-parted calyces, 315

TABLE I

	2	3	4	5	6	7	8	9	
Sepals.....	0	9	315	–	226	17	1	0	568
Petals.....	0	6	355	–	283	15	0	1	660
Stamens.....	0	6	330	–	228	10	0	1	575
Carpels.....	49	–	197	4	1	0	0	0	251

had 4-parted calyces, etc.; the total, in the right-hand column, shows that 568 of 839 variants were abnormal as to calyx. The table demonstrates that most variations consist merely in the addition or removal of one member of any whorl,—much less often, two members, and only rarely more than that. For some observers this is the

[10] Witte, H., "Ueber abweichende Zahlenverhältnisse und einige andere Anomalien der Blüten der *Campanula rotundifolia* L.," *Arkiv för Botanik,* 1905, Bd. 4, N: o 17.

Dahlgren, K. V. O., "Studier öfver afvikande talförhållanden och andra anomalier i blommorna hos några Campanulaarter," *Ark. f. Bot.,* 1911, Bd. 10, N: o 10. For a translation of this paper, the writer is much indebted to Miss Ruth Berggren.

whole significance of these variations. With the carpels the tendency to increase rather than decrease greatly predominates in all four species. To a less extent the same tendency prevails in the outer whorls of *C. rotundifolia.* But the other species severally, and all four taken together as seen in the table, have a reduced number of sepals, petals and stamens more often than an increased number. The number of petals is somewhat more subject to variation than that of stamens or sepals, in Dahlgren's list. But the carpels are clearly the most fixed and conservative element in the flower, variations in any other whorl being more than twice as frequent. Even the stigmas vary more than the carpels, for Dahlgren found 50 flowers in which the number of stigmas and carpels did not agree, and in 46 of these the number of carpels was normal.[11] Witte previously had noted that a style with either two or four stigmas might proceed from a normal 3-celled capsule.

The appearance of some of the variants of *C. rapunculoides* is shown in Fig. 2, with a raceme of normal flowers at *A* (formula, or number of parts in the successive whorls, 5, 5, 5, 3). Symmetrical flowers may be produced by increasing the carpels and stigmas to five, the first step in the process being apparently the formation of four stigmas. In the three allied species Dahlgren found 28 flowers with four stigmas but only three carpels. Next would occur 4-carpellate, 4-stigmatate forms, of which he observed 104 examples (Fig. 2 *c*). Apparently the upper loculus of the 3-celled ovary usually widens (Fig. 1 *h*), and then becomes divided, with some readjustment of the septa, in making the four carpels (Fig. 1 *g*). The septa are rarely, if ever, placed with geometrical precision. The distribution of the carinal veins in the carpel-walls may be exactly like that in De Candolle's variant of *C. medium* (Fig. 1 *f*). Such flowers presumably represent the stages traversed in

[11] The flowers with 5 sepals, petals, and stamens, and 3 carpels, but with an abnormal number of stigmas, have not been included in the above tabulation. There were 33 of these.

making the antisepalous form of the completely symmetrical pentamerous campanula, and thus the evolution of a distinct section of the genus seems primarily a matter of symmetry. Dahlgren found one 5, 5, 5, 4 flower of *C. patula* with 5 stigmas, and two flowers—one of that species and one *C. rotundifolia*—which were completely pentamerous. The unstable forms with formula 5, 5, 5, 4, though common variants, are apparently not normal for any species of Campanula, nor characteristic of any related genus.

It seems not improbable that species with five carpels alternating with the stamens (and so opposite the petals, or "antipetalous") were likewise derived from tricarpellate flowers by a different arrangement of the septa, rather than by the suppression of a hypothetical circle of stamens. For the septa may extend either to the carinal veins (note the upper septa in Fig. 1 *h*) or to the sutural veins (as below in Fig. 1 *g*). If all the septa should be of one or the other of these types, the flowers would become antipetalous or antisepalous accordingly. Again, the lower right carpel in Fig. 1 *B* is almost perfectly antipetalous. The others need only become like it to produce flowers generically distinct from the form in Fig. 1 *A*. Or, should the arrangement of the three carpels in Fig. 1 *B* be inverted, as sometimes happens, and the median lower cell enlarge and subdivide as the median upper one seems to do normally, then the carpels would be antipetalous. In fact, five such antipetalous carpels may actually be produced as variants of *C. persicifolia*, according to Penzig (*l. c.*, p. 537). It appears, therefore, that the evolution of the antipetalous pentacarpellate genus Platycodon, like that of the antisepalous pentacarpellate species of the *C. medium* type, is essentially the attainment of symmetry from or through the tricarpellate form.

A different sort of symmetrical flower, not found normally in any species of Campanula, but representing what may perhaps, at some future time, be specifically

distinct, occurs as a common variant of *C. rapunculoides*. Among some plants growing without cultivation around a long-abandoned garden, the writer found, in 1896, that in 31 out of 367 flowers examined, there were 3 carpels, 6 stamens, 6 petals, and a more or less 6-parted calyx, the flowers being quite symmetrical on the plan of three (Fig. 1 *C*). Later some twenty more such flowers were found, including the stalk in Fig. 2 *B*, which bears seven of them. It has also—the second from below—a 6, 6, 6, 4 form. The lowest bud is 6-parted; four others are 5-parted and one—the fourth from the top—is 4-parted. It seems a general rule that the lower flowers may be 5-parted; then, and often with some variations, the 6, 6, 6, 3 form is attained and held; with finally, toward the top of the stem, a falling off to the pentamerous form. Certain individual plants or groups of plants show this tendency, sometimes to such an extent that 6, 6, 6, 3 flowers predominate. The increase of parts may begin in the calyx, a lobe of which, and apparently not always the same one, becomes split. The parts diverge and the other sepals become rearranged to make an even 6-pointed star (Fig. 1 *k-l*). Meanwhile the stamens and petals have added a member, sometimes in advance of the calyx. Dahlgren found in the four species the following combinations: 6, 5, 5, 3–15 flowers; 6, 6, 5, 3–26 flowers; 6, 6, 6, 3–109 flowers. But he found also 5, 6, 5, 3–19 flowers; 5, 6, 6, 3–37 flowers; which indicate that the initiative is somewhat more often in the corolla than in the calyx. No flower was found of the formula 5, 5, 6, 3, so that the stamens are clearly not an active factor.

The flowers of the formula 6, 6, 6, 3 prove to be, on section of the ovary, not as symmetrical as might be expected. Usually one cell is much the largest, and may contain six of the twelve veins in its wall (Fig. 1 *C*). Although cells nearly equal in size have been seen, in no case have the septa passed symmetrically to three carinal or three sutural veins. But such flowers may yet be found, since the requisite readjustment is sometimes

slight. Probably correlated with the width of the upper carpel there is a tendency for the 6-parted flowers to produce four carpels, one instance of which has already been noted. Dahlgren found 51 of these flowers. If two opposite carpels should be antipetalous and the other two antisepalous, a remarkably symmetrical form would result, but such perfection has not been observed. A single flower of the 6, 6, 6, 5 pattern was found by Dahlgren, but not one with all its parts in sixes, as is characteristic of the campanulate genus Canarina. That coarse aberrant form, of the Canary Islands, is, however, often pentamerous, and from such a type it presumably developed. Often *C. rapunculoides* and its allies go beyond the hexamerous arrangement, producing a wide scattering of unsymmetrical combinations. Of these the most frequent is probably 7, 6, 6, 3, of which Dahlgren saw five examples. Witte describes a single plant of *C. rotundifolia* in which 28 out of 32 blossoms were abnormal, and 14 of them had gone beyond 6, 6, 6, 3 to 7, 6, 6, 3; 7, 7, 6, 3; 7, 7, 7, 3; 8, 6, 6, 3, etc. It appears very strikingly in Dahlgren's table, however, that most of these higher unsymmetrical combinations are represented, among the 839 variants, by single specimens only, and none by more than five cases. There is no record of a completely 8-merous flower, with 8 carpels and 8 stigmas, such as is normal in the small campanulate genus Michauxia. It may be regarded as an indication of a recently acquired and difficult symmetry that the flowers of Michauxia are notably subject to numerical variation (Penzig).

Having considered the ways in which the asymmetrical tricarpellate campanulas may and do acquire symmetry by the increase of their parts, there remain to be presented the variations involving reduction. Rather unfrequently in *C. rapunculoides* the carpels and stigmas are reduced to two in an otherwise normal flower (Fig. 2 *d*). The carpels are usually placed one above the other, each having five veins in its wall and being to this

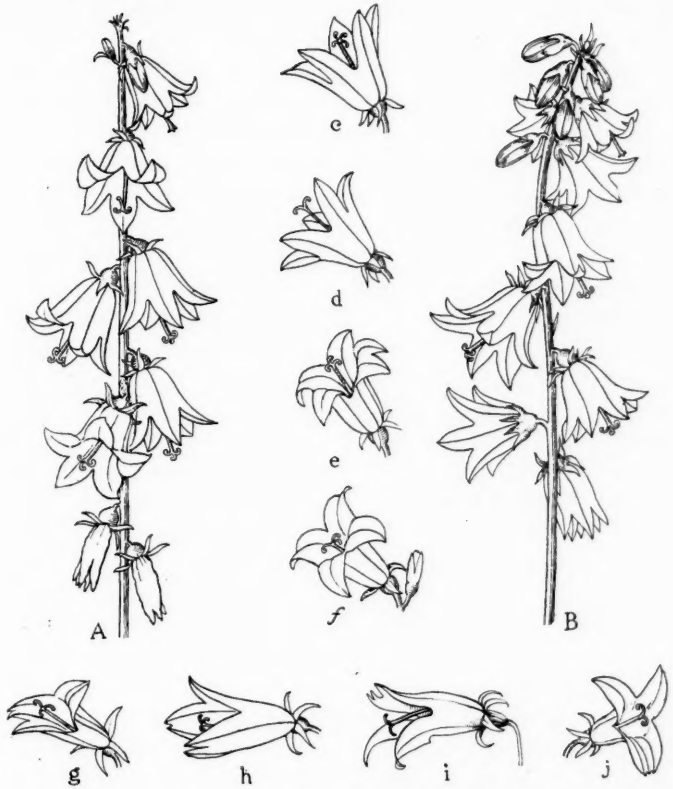

FIG. 2. Numerical variations in the flowers of *C. rapunculoides*. *A*, normal 5, 5, 5, 3 flowers; *B*, the nearly symmetrical 6, 6, 6, 3 variant; *c*, the 5, 5, 5, 4 form; *d*, 5, 5, 5, 2; *e*, 5, 5–4, 5, 3; *f*, 4, 4, 4, 3; *g*, one wide and three normal sepals, 2-tipped corolla, 5 stamens, 3 stigmas; *h*, 5 sepals, tripartite corolla, 5 stamens, 3 stigmas; *i* and *j*, 5, 5, 5, 2 flowers with corollas suggestive of lobelia, the broad 3-toothed segment of the corolla being above in *i*, and below in *j*. (Drawn by Miss Mabel Herford, except *i* which is by Mr. H. F. Aitken.)

extent symmetrical (Fig. 1 *i*); but they generally vary in size and their axis may be at an angle with the vertical. Dahlgren records 18 flowers with the formula 5, 5, 5, 2. It is a change taking place in the allied genus Phyteuma, in which De Candolle described 15 species with 3 carpels; 10 species with "3, sometimes 2," or *vice versa;* and 3 species with 2 stigmas and bilocular capsules. In another

allied genus, Jasione, the species are all of the 5, 5, 5, 2 type.

More frequently, in the campanula-variants, the members of the outer whorls are reduced to four, while the three carpels remain unaltered. In producing flowers of the 4, 4, 4, 3 type (Fig. 2 *f*) two petals may fuse, as in Fig. 2 *e*, and the calyx may show such intermediate stages as in Fig. 1 *k–j*. Of what may be regarded as stages in its production, Dahlgren records the following combinations, here followed by the number of flowers of each kind which he observed; 4, 5, 5, 3–29; 4, 4, 5, 3–7; 5, 4, 5, 3–14; 5, 4, 4, 3–39; but no instance of 5, 5, 4, 3. As with the increase in the outer whorls, the initiative is never with the stamens; it is often with the calyx, but distinctly more often with the corolla. The resulting unsymmetrical flower (4, 4, 4, 3) not normal for any campanulate species or genus, Dahlgren found to be the commonest variant, yielding 247 examples. It becomes symmetrical when the carpels are reduced to two, but only fifteen such flowers were found. Further reductions lead to the form 3, 3, 3, 2, of which a single example is listed, but as shown in one of Dahlgren's figures, the trimerous corolla may be perfectly formed, without bifid lobes or other evidence of its pentamerous derivation. In the related genus Wahlenbergia, which has been called the Campanula of the southern hemisphere, there are some completely pentamerous species and many of the 5, 5, 5, 3 type, but in *W. lobelioides* the features of the variant just described have become specific characters. De Candolle (*l. c.*, p. 158) says of *W. lobelioides:* "The calyx-lobes are often 3 but sometimes 4 or 5; their number seems to be greater in earlier flowers. The corolla, usually 3-cleft, but sometimes 4- or 5-cleft, varies less than the calyx. I have found the stamens always 3, and the cells of the capsule 2." But this is neither a very symmetrical nor a very stable arrangement.

Some reduced forms of *C. rapunculoides* are shown in Fig. 2 *g–j*, all of which came from a small group of uncultivated plants on the site of the Boston Lying-in

Hospital. No such flowers were seen during several years in another patch which yielded many 6, 6, 6, 3 blossoms, and they probably are quite unusual. Magnus has noted that polymerous flowers of other campanulas are "not rare in certain localities,"[12] but what leads to the local production of particular variants is past speculation. The distorted flower in Fig. 2 *g* has 3 stigmas, 5 stamens, a somewhat bilabiate corolla (due to the fusion of 2 and 3 petals, respectively), and a 4-cleft calyx. The tripartite corolla of Fig. 2 *h* results from the fusion of two pairs of adjacent petals, one petal remaining separate. This flower had 3 stigmas, 5 stamens, and 5 sepals. Another flower, not drawn, of the 5, 5, 5, 3 formula, had a tripartite corolla with the three lower petals fused and the two upper ones separate. Tripartite corollas were found also in three flowers with two stigmas. In one of these the segment of the corolla formed by the fusion of three petals was above, as the flower extended out from the stem (Fig. 2 *i*); in the other two it was below. These two differed as to their stigmas, which were transversely placed in a flower not drawn, but were nearly vertical in the other (Fig. 2 *j*). This flower has acquired essentially the form and bilateral symmetry of Lobelia, which, as exemplified in *L. inflata*, is illustrated in Fig. 3.

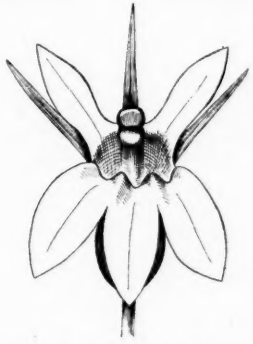

FIG. 3. The symmetry of *Lobelia inflata* L. Enlarged 6 diameters. (Author's sketch redrawn by Mr. Aitken.)

[12] Magnus, *Verh. d. bot. Vereins d. Prov. Brandenburg*, Jahrg. 18, Sitz.-ber. vom 28 Juli, 1876, p. 111.

Notwithstanding the great difference in the form of flowers of Campanula and Lobelia, it has long been recognized that these genera are very closely allied. Jussieu placed them both in the Campanulaceæ in his "Genera Plantarum" of 1789, where Robert Brown left them, after extracting the "Stylideæ" and "Goodenoviæ" in 1810. They remain together in the Campanulaceæ of Schönland (Engler u. Prantl, Pflanzenfamilien, 1894). In Lobelia, apart from the different symmetry of the flower, the anthers have fused with one another in a ring about the style; and on one side, between two petals, the corolla is split its whole length. But the anthers of Campanula stand close together in the bud, and are somewhat fused in Jasione, and fully fused in three species which De Candolle removed from Campanula to his genus Symphandra. A corolla split down one side occurs as a variation in an otherwise normal flower of *C. rotundifolia,* well figured by Witte, and Dahlgren shows other instances. A further distinction between Campanula and Lobelia, first pointed out by Brown, is that the flowers of Lobelia in the bud take a very unusual position, by having a median sepal below and a petal in the midline above; but when these buds have opened, the flower stalk has twisted and the flower has been rotated to the usual position, with a median sepal uppermost. There seems to be some twisting in Campanula, but nothing as definite and pronounced as the "resupination" of Lobelia. It appears, therefore, that the flower in Fig. 2 *h* may be more like a lobelia than that in Fig 2 *i,* neither stem showing obvious twisting.

In reviewing what has been said of variations in Campanula, we are persuaded that symmetry is the expression of factors dominant in evolution. The principal types centering about the imperfectly symmetrical and consequently very variable tricarpellate campanulas are attainments of more symmetrical and sometimes more stable forms. Of these there have been mentioned the antisepalous pentamerous type of *C. medium;* the antipetalous pentamerous Platycodon; the hexamerous Canarina and octamerous Michauxia; the symmetrical 6, 6, 6, 3 form not as yet characteristic of any species; the 5, 5, 5, 2 type in Phyteuma and Jasione; and finally the rearrangement of the lobes of the corolla in that type, with the attainment of bilateral symmetry. This in some early group of campanulaceous plants was a momentous event in botanical evolution, leading to the lobelias and thence to the Compositæ, and changing in some seasons and places the entire aspect of vegetation.

If this interpretation seems too inadequate and overborne by the innumerable exceptions to symmetrical productions, is it not more simple and intelligible than to derive bilateral flowers from the radial "through a long course of slow modification,—each modification having been preserved which was useful to the plant?" Certainly Darwin's alternative is not strengthened when Spencer defends it as follows ("Principles of Biology," 1867, Vol. 2, Ch. X):

> If we bear in mind the functions of flowers, we shall find in their adaptations to their functions, under conditions that are extremely varied, an adequate cause for the different types of symmetry. . . . We shall find reason for concluding that the forms and positions of those subsidiary parts which give general shape to the flower arise by the survival of individuals which have the subsidiary parts so adjusted as to aid in the process of fertilization—the deviations from radial symmetry being among such adjustments. . . . So long as the axis of a flower is vertical, a bee or butterfly alighting on it will be as likely to come from one side as from another. . . . But a bee or butterfly coming to a laterally-growing flower . . . almost of necessity settles with the axis of its body inclined upwards towards the stem of the plant. . . . We see that a long undermost petal or lip by enabling the insect to settle in such a way as to bring its head opposite the opening of the tube, aids its fertilizing agency. But whatever be the special modifications of the corolla which facilitate the actions of the particular insects concerned, all of them will conduce to bilateral symmetry.

To ascribe the production of the bilateral flower in Campanula to the direction of the approach of bees is perhaps as diverting as anything in medieval physiology and supports Russell in doubting whether the whole theory of natural selection is properly applicable to problems of form.[13]

Symmetry in the Aortic Arches

After having seen in Campanula, and in other plants, the passage from one form of symmetry, through an intermediate asymmetrical condition, to symmetry of a new sort, some example of a similar process was sought in mammalian development. The transformation of the aortic arches in the sheep seemed to be an instance of this

[13] Russell, E. S., "Form and Function," London, 1916, p. 232.

kind, and the critical stages having been selected, Dr. G. H. Jackson, Jr., made a series of models of the vessels, drawings of which will here be presented. The labor and skill required were considerable, and the results show more extraordinary migrations of blood-vessels than have hitherto been recorded. For the privilege of presenting this story, the author is greatly indebted to his collaborator, Dr. Jackson. The drawings (Figs. 4–7) are all ventral views, in which the observer is looking at the arteries in the front of the thorax and neck.

At a certain stage in embryonic development in mammals generally, the blood leaves the heart by two more or less median ventral vessels, the aorta and pulmonary artery (Fig. 4, ao. and a. p.). From them the blood is conveyed to the back of the body by a series of bilaterally symmetrical arched vessels known as the aortic arches, and these empty into two longitudinal trunks, one on either side,—the dorsal aortæ (Fig. 4, ao. d.). The dorsal aortæ unite in the midline below, giving off the subclavian arteries, to the front limbs, shortly before their union. The pulmonary artery divides into the two pulmonary arches, from each of which a vessel descends to the corresponding lung. The aorta divides, somewhat indirectly, into two aortic arches on either side, which are known as the third and fourth arches, respectively. Anterior to them, in earlier stages, were the first and second arches which have now disappeared. The dorsal aortæ are continued up the neck as the internal carotid arteries; and ventrally, from the root of each third arch, an external carotid artery likewise passes up the neck. Except where the aorta and pulmonary artery leave the heart, this system of vessels is strikingly symmetrical, with a symmetry characteristic of the corresponding arteries in adult fishes. In mammalian embryos this pattern, with slight variations, everywhere prevails. But it gives rise to a great variety of arrangements in the adult, some of which are symmetrical or nearly so, but others are far from symmetry. With the growth of the sheep embryo, and the great elongation of

the thoracic and cervical regions, the original symmetry is soon lost.

In the sheep of 14 mm. (Fig. 5), by comparison with the younger stage (10 mm.), the following changes may be noted. The subclavian arteries now leave the dorsal aortæ much higher up than before—the distance from their origin to the place where the dorsal aortæ come together below is now considerable. Moreover, the part of the right dorsal aorta between the subclavian artery and the aortic junction has been reduced to a strand, and in the next stage will have disappeared altogether. After that has taken place, the right dorsal aorta from the fourth arch to the origin of the subclavian artery is considered a part of the right subclavian artery. The right pulmonary arch has gone already, except as it is represented by the bend in the root of the branch to the right lung. The fourth arches have become very short and are no longer opposite each other, since on the right the confluence of the third and fourth arches with the main aorta has been drawn out and directed upward. The passage from the fourth to the third arch on either side has become greatly elongated, but more so on the left, and the resulting vessels may now be called the common carotid arteries. Each of them divides into the external carotid artery and the third arch, which arch, from now on, constitutes a part of the internal carotid artery. From the internal carotid artery proper to the fourth arch, the dorsal aorta on either side has become very long and slender; with its total disappearance in the next stage, the picture becomes greatly simplified.

At 18 mm. the arterial trunks of the sheep have the very unsymmetrical arrangement seen in Fig. 6, in which the following changes have taken place. The branches of the pulmonary artery to the right and left lungs now leave the pulmonary arch by a common stem, presumably an elongation of the place of their adjacent origin. The left subclavian artery has traveled up, beyond the pulmonary arch, to the root of a vessel marked "*x*," which deserves particular attention. It is a long main trunk prolonged from the region "*x*" of the preced-

ing stage. Since it divides into vessels for the arm and head, it is named the brachiocephalic artery, but at this stage the vessel for the left arm, although at its root, is still independent. The way in which the left subclavian artery has moved along the aorta to its new position is quite remarkable, and seems due to a rearrangement of cells around its orifice, spreading apart above and closing in below. The common carotid arteries

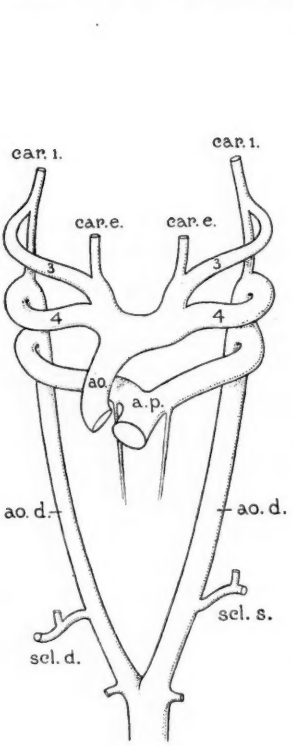

Fig. 4

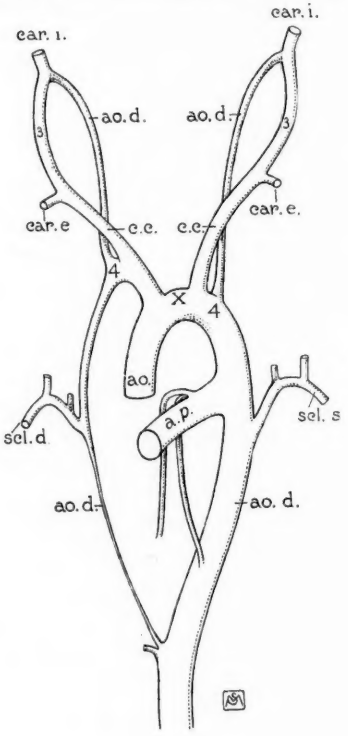

Fig. 5

FIGS. 4–7. The development of the aortic arches of the sheep as seen in ventral view. Fig. 4, embryo of 10 mm. (Harvard Embryological Collection, Series 1232). Fig. 5, embryo of 14 mm. (H. E. C., Ser. 1106). *Ao.*, arch of the aorta as it leaves the heart; *ao. d.*, dorsal aorta; *a. p.*, pulmonary artery; *car. e.*, external carotid artery; *car. i.*, internal carotid; *c. c.*, common carotid; *scl. d.*, right subclavian artery; *scl. s.*, left subclavian; *3* and *4*, third and fourth aortic arches. *x* and *v* mark corresponding vessels in the successive figures, as explained in the text.

have become very long, and their bifurcation into external and internal carotids is now far up the neck. With the disappearance of the dorsal aorta on the right, the fourth arch has become an unrecognizable part of the right subclavian artery (at the position marked 4); the

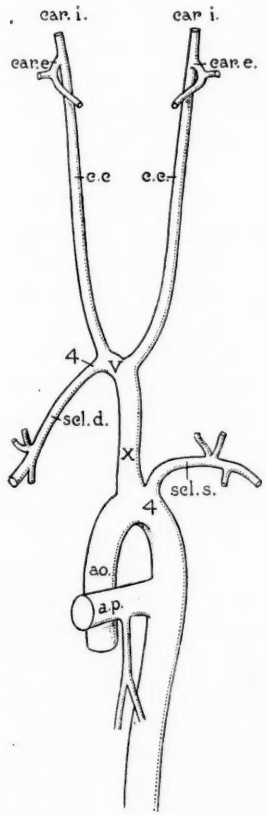

Fig. 6

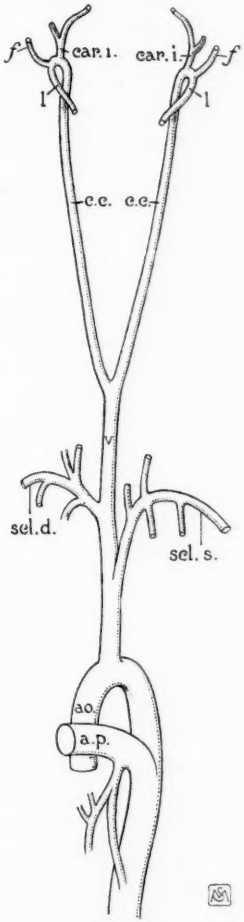

Fig. 7

Fig. 6. Sheep embryo of 18 mm. (H. E. C., Ser. 1238). Fig. 7. Sheep embryo of 47.5 mm. (H. E. C., Ser. 1696). *f*, facial artery; *l*, lingual artery. For explanation of other lettering, see opposite page. Figs. 4–7 are from models by Dr. G. H. Jackson, Jr., sketched by F. T. Lewis in simplified form, so that the following magnifications are only approximate. Fig. 4, × 35 diam.; Fig. 5, × 30 diam.; Fig. 6, × 25 diam.; Fig. 7, × 8 diam.

left fourth arch is merged in the main arch of the aorta, without demarcation, presumably at the place likewise marked 4.

In such large sheep embryos as shown in Fig. 7 (47.5 mm.), a new symmetry has almost been attained, if the origin of the vessels from the heart be disregarded. A median brachiocephalic artery extends up the neck, along which the left subclavian artery has climbed to a point nearly opposite the right subclavian. This is followed by a median vessel "*v*," sometimes called the "cephalic" or "bicarotid trunk," which divides into the two common carotid arteries. It has been extended from the region "*v*" of the preceding stage. Each common carotid divides into the small internal carotid arteries and the very short external carotids; the latter divide at once into facial and lingual branches (*f* and *l*), which were seen in the preceding stage. This entire arrangement stops just short of the attainment of symmetry, for in the adult there is usually an interval, sometimes half an inch, between the points at which the subclavian vessels leave the brachiocephalic trunk. The slight shifting which would eliminate this interval would lead to perfect symmetry, far removed from that equally perfect symmetry from which it came.

The principal types of origin of the mammalian subclavian and carotid arteries from the arch of the aorta are shown in the diagrams in Fig. 8, which include all the symmetrical forms, *A, D, E* and *F,* with two quite unsymmetrical,—*B* and *C*. Similar diagrams are found in many books, but the best account of the occurrence of the various patterns is perhaps that of Parsons.[14] He writes: "I have for a good many years wondered what cause or causes determined the various arrangements of the great trunks arising from the arch of the aorta," and to find this out he dissected extensive zoological material and studied the literature. He decided that "nearness of kin does not seem to play any great part in determining

[14] Parsons, F. G., "On the Arrangement of the Branches of the Mammalian Aortic Arch," *Journ. of Anat. and Physiol.*, 1902, Vol. 36, p. 389–399.

the arrangement of these branches'' and comments on the wide variation within a single species. ''The commonest mammalian arrangement,'' he finds, ''is that in which the left carotid rises from the base of the innominate''—a form intermediate between Fig. 8 *B* and *C*, the left carotid having fused with the innominate only low down and sufficiently to provide a common outlet. ''From this,'' he declares, ''the variations range in two directions, either toward concentration or separation of branches.'' Embryologically, however, the form in Fig. 8 *C* is more primitive, representing as it does an arrest of development at the stage of Fig. 5. It can, therefore, more logically be regarded as the center of divergent variations. This arrangement, with greater or less distance between the left subclavian and the left common carotid, is found, according to Parsons, in ornithorhynchus and echidna, in some marsupials (*e.g.*, the wombat), some edentates (armadillo and pangolin), in the dugong, in the beaver and occasionally in rabbits, in seals (but not in other carnivora), in several of the insectivora, sometimes in various monkeys, and as the normal arrangement in man. The variations in monkeys and in man have been tabulated by Sir Arthur Keith,[15] in whose judgment they form a series *progressing toward* the typical human arrangement (Fig. 8 *C*), which we regard as primitive and a point of departure.

An interesting symmetry may be attained if, beginning at the stage of Fig. 5, the left subclavian vessel should travel up the left common carotid artery to a point opposite the right fourth arch. Development without further changes would produce the arrangement in Fig. 8 *D*. This is acquired in certain of the insectivora. It is ascribed to the mole (Talpa) without exception. Parsons records it in one out of two golden moles (Chrysochloris) and in one out of three hedgehogs, the others having the primitive arrangement of Fig. 8 *C*, which is the only distribution attributed to certain other species, such as

[15] Keith, A., ''The Modes of Origin of the Carotid and Subclavian Arteries from the Arch of the Aorta in Some of the Higher Primates,'' *Journ. of Anat. and Physiol.*, 1895, Vol. 29, p. 453–458.

the desman (Myogale). In the bats "all authors seem agreed that the symmetrical bi-innominate arrangement is the constant one," and among cetaceans, insufficiently investigated, Parsons finds it "very common if not the commonest" distribution. It was found once as an anomaly in the chimpanzee,[16] and may occur in man, Poynter citing nine recorded cases.[17] Kopsch, in Rauber's Lehrbuch, 1906, states that the formation of two innominate trunks is "the most frequent variation" (in man) but this is contrary to all opinion. Wherever it occurs, it affords a perfect instance of the passage from one symmetry to another through an intermediate stage of disorganization.

FIG. 8. Diagrams of the origin of the subclavian and carotid arteries from the arch of the aorta in adult mammals. *A*, the type already shown in Fig. 7. *B*, approximately a persistence of the stage in Fig. 6. *C*, arrest of development at the stage of Fig. 5. *D*, *E*, and *F* (with *A*) represent the symmetrical arrangements sometimes attained, as described in the text.

The great majority of mammals start toward that type of symmetry nearly attained in the sheep. The first step is the slight fusion of the left common carotid artery with the innominate, "man's commonest abnormality," according to Parsons, with a frequency of 1 in 10. It is normal for the rabbit and guinea pig. With greater fusion, extending almost, but not quite, to the level of the right subclavian, it corresponds with an arrest of development at the stage shown in Fig. 6. With slight variations this may give rise to three adult forms. The brachiocephalic artery may divide into a very short in-

[16] Chapman, H. C., "On the Structure of the Chimpanzee," *Proc. Acad. Nat. Sci.*, Philadelphia, 1879, p. 57–58.

[17] Poynter, C. W. M., "Arterial Anomalies Pertaining to the Aortic Arches," *University Studies*, Lincoln, Nebraska, 1916, Vol. 16, 116 pp.

nominate and a left common carotid (form *a*,—Fig. 6); or the brachiocephalic may divide at once into three terminal branches (form *b*,—Fig. 8 *B*); or a slight median extension may produce a short bicarotid artery (form *c*). The distinction between the aforesaid forms *a* and *c* is carefully drawn by Parsons, though it seems to be without special significance. Of the kangaroo Macropus, two specimens were of form *a* and one of form *c;* the lion and ocelot have form *a*, and the tiger and leopard, form *c*. Some rodents and some monkeys present these arrangements, which, however, are specially characteristic of the carnivora and the pig; with a long bicarotid added, Fig. 8 *B* would represent the condition in the llama and giraffe.

The final stages toward the symmetry of the sheep (Fig. 8 *A*) are, first, those in which the left subclavian begins to climb the brachiocephalic trunk. Such beginnings were found by Parsons in a few rodents (as the agouti) and sometimes in the genet (the only instance in the carnivora), but in these orders progress toward symmetry stops at that point. This initial stage is recorded also for the rhinoceros, gazelles, and antelopes, and in a single lemur among twelve (the others forming a progressive series from the type of Fig. 8 *C* through that of Fig. 8 *B*). The sheep, goat, and cow reach the form shown in Fig. 8 *A*, which is nearly attained in the horse.[18] But, as already noted, no careful description indicates that the two subclavian arteries are ever placed at exactly the same level.

The other symmetrical displays (Fig. 8 *E* and *F*) have been well illustrated in human anomalies, but are very exceptional as normal arrangements. Keith regards Fig. 8 *E* as "the natural climax" of the series in the higher Primates. It doubtless arises at an early stage (Fig. 4) by a deepening of the ventral cleft between the right third and fourth arches, followed by an arrest of development. Parsons found it once in the marsupial

[18] The primitive arrangement (Fig. 8 C) may be expected in these animals as anomalies. A perfect example, in a donkey, was reported by Huytra as cited by Skoda (*Anat. Anz.*, 1912, Bd. 40, p. 542, Fig. 5).

bear (Koala), but he does not record it for cetaceans as is often done. The form in Fig. 8 *F* has been found in the marsupial wolf of Tasmania, and by Cuvier in an elephant, but the elephant is said usually to have the arrangement in "man's commonest anomaly," namely an innominate joined at its base by the left common carotid. It seems unprofitable to speculate concerning its development, but the deepened ventral cleft in the stage of Fig. 4 would separate the right subclavian artery, and a subsequent elongation of the region "*x*" in Fig. 5 would produce a bicarotid vessel.

Before concluding that symmetry is the objective of all the variations which have now been presented, certain other interpretations must be considered. Concerning that "commonest variation in man" which we have regarded as a first step toward the symmetry of ruminants, less advanced than that taken by some monkeys, Sir Arthur Keith has said: "It is doubtful if one can legitimately construe this apparently cynomorphous reversion in Man as an atavistic tendency"—with which we fully agree, but he continues,—"more probably it has no more morphological worth than the degree of interdigital webbing." Although he thus makes the variations within a species of no moment, he believes "that the type prevailing in each genus in all probability best serves the body-economy of that genus, but how it does so is by no means clear." Since the frequent radical departures from the prevailing type occur without apparent detriment to the individual, this becomes an interesting profession of faith. As suggesting the way in which a particular plan of branching may be most appropriate for a given species, there is little to be added to Professor Owen's comments, in 1868, here quoted with references to our own figures whenever appropriate.[19]

In the non-claviculate narrow-chested Ungulates the varieties *A* and *B* (Fig. 8) are met with, that of *A* prevailing: in non-claviculate but broader-chested Unguiculates, with flexile and rotatory fore limbs, the separate origin of the left brachial is more constant and remote from the innominata: the same is better marked in the broader-chested Swimmers (*Lutra, Phocæna*) and in the claviculate

[19] Owen, R., "On the Anatomy of Vertebrates," Vol. 3, 1868, p. 537.

Quadrumana: in many *Insectivora* an analogous but other arrangement prevails (Fig. 8 *D*). In the broad-chested species illustrating the variety *C,* the head and pectoral limbs are supplied by three primary trunks: in the still broader and flatter-chested *Sirenia* the heart itself is able to expand laterally, even to a partial severance of the ventricles, the aortic arch shows its widest span, and the intervals between the innominata, the left carotid and the left brachial are longer.

Parsons in confirmation writes: "It would be quite easy, had I the space, to multiply examples showing the coincidence between a broad thorax and its outlet on the one hand, and separation of aortic branches on the other; these examples are so numerous that it seems justifiable to regard the arrangements as cause and effect."

No one, however, has shown which is the cause and which the effect. The arteries in their development precede the bony outlet of the chest, which very possibly conforms to their arrangement. And in man, with, so far as known, a uniform outlet, all the types have been found, though of that in Fig. 8 *A* only an imperfect example, the picture of which has been repeatedly copied (see Poynter's Fig. 37). In the bat, cited by Parsons as having a very wide thoracic outlet, there are but two trunks as in the "non-claviculate, narrow-chested" pig. Thus the interesting correlation between the diameter of the outlet and the number and spacing of the vessels passing through it, does not seem to account for the symmetrical and asymmetrical arrangements under discussion.

Returning to the hypothesis of symmetry as an end and aim of these designs, the relation of the arteries to the corresponding veins must be considered. For the veins, like the arteries, begin as symmetrical paired vessels, though totally different in their arrangement. Through ready and frequent anastomoses and atrophy of parts, they shift more freely than the arteries, and acquire a new symmetry quite closely conforming to that of the arterial system. As seen by comparing Figs. 9, 10 and 11, this conformity is most exact in the sheep (Fig. 9) and one wonders the more why the left subclavian artery has not traveled a half-inch higher to

perfect the symmetry. In the pig (Fig. 10) the veins have made a pattern which would be much more closely followed by the arteries if the left subclavian artery should ascend the brachiocephalic. That further departure from the embryonic status has not as yet been effected, but is it unreasonable to suppose that in a geological

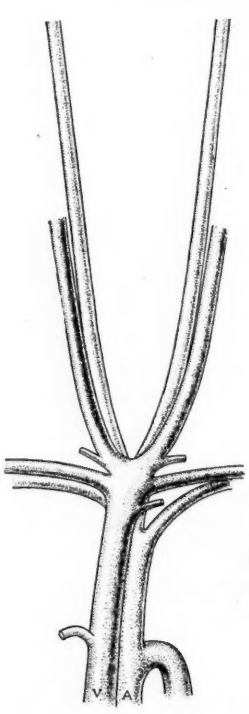

Fig 9

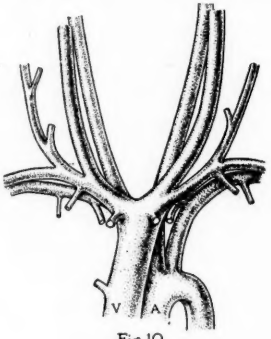

Fig. 10

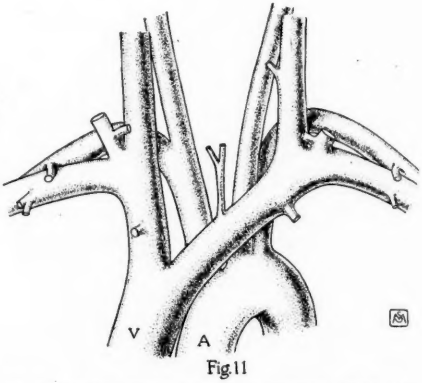

Fig.11

FIGS. 9–11. The jugular and subclavian veins shown in relation with the carotid and subclavian arteries, together with the main trunks from which they proceed, and the beginnings of certain branches; *A*, arteries; *V*, veins. Fig. 9, the pattern of these vessels in the sheep; Fig. 10, in the pig; Fig. 11 (modified from Sobotta's Atlas), in man.

period it may be brought about? In man (Fig. 11) the distribution is still less perfect and two possibilities for symmetry are apparent. It would seem to be more readily attained by the formation of a left innominate vessel as happens in some anomalies; but the trend seems rather

toward fusion of the left carotid with the innominate, thus starting upon the path already traversed in the pig and sheep. Whether or not either of these forms of symmetry may ever be attained is a question which we do not attempt to answer.

Having considered symmetry as a factor in the arrangement of these minor parts, something should perhaps be said concerning the disposition of the major viscera, where symmetry indeed seems to have lost control.

The Dextral Spiral of the Viscera

In the young mammalian embryo, bilateral symmetry prevails not only in the larger vessels, but in the heart itself, and in the digestive tube with all its appendages. For comparison with the later stage the diagrammatic ventral view, Fig. 12, may serve, though it is very far from resembling the actual appearance of any embryo. Above, the heart is shown as a median tube, bent so that its venous end is dorsal and its arterial end ventral. Below the diaphragm, an outline suggests the median position of the stomach, characteristic of its earliest stages. For a longer time the liver, in ventral aspect, is median and perfectly symmetrical, and below it, the gall-bladder is primarily in the midline. The ventral pancreas has symmetrical right and left lobes, which some regard as separate glands, and the dorsal pancreas at the outset is also bilaterally symmetrical.[20] The intestine forms a loop extending ventrally. Its upper limb is small intestine, which makes the bend and ends at the cæcum on the lower limb, the remainder of which is large intestine. Subsequently all these organs are involved in a dextral rotation, similar in direction to that of gastropod molluscs, producing the adult condition shown in Fig. 13. The cardiac loop and the intestinal loop, it will be noted, bend in precisely the same manner.

The dextral nature of the torsion of the primary loop

[20] These relations of the pancreas are further described in the *Amer. Journ. of Anat.*, 1911, Vol. 12, p. 389–400.

of intestine as seen in Fig. 13 would become more evident if it were carried a half-turn further, as actually occurs in the pig. Such a condition is diagrammatically shown in Fig. 12 *c*, but has been very accurately drawn by Dr. Lineback in connection with his study of the remarkable

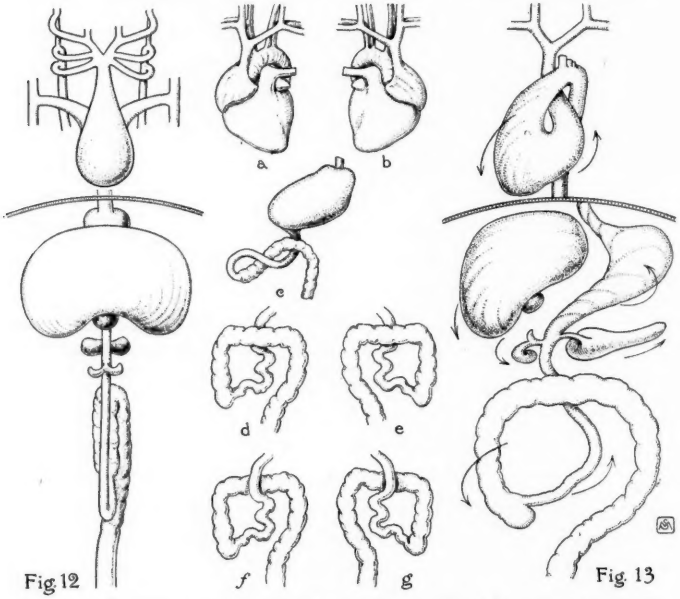

Fig. 12 Fig. 13

FIG. 12. Diagram of the primitive bilaterally symmetrical disposition of the human viscera. Fig. 13, diagram of the adult arrangement resulting from a dextral rotation. Fig. 12, *a*, the normal heart and vessels; *b*, the same structures in situs inversus; *c*, diagram of the more extensive rotation of the primary loop of intestine as it occurs in the pig; *d*, the normal relation of the human colon and small intestine; *e*, their relatively frequent relation in situs inversus; *f*, retroposition of the colon in situs solitus, a very rare anomaly; *g*, retroposition in situs inversus, apparently never observed. It should be noted that *d* and *g* are dextrally rotated; *e* and *f*, sinistrally.

spiral coil in the colon of the pig.[21] In the pig the colon forms a dextrally coiled mass of three or four complete revolutions, rarely winding sinistrally. The primary loop of intestine may also rotate sinistrally, but very rarely. If this primary loop should remain directed forward or ventrally, there would be but two possible arrangements in the adult, dextral and sinistral, respec-

[21] Lineback, P. E., "The Development of the Spiral Coil in the Large Intestine of the Pig," *Amer. Journ. Anat.*, 1916, Vol. 20, p. 483–503.

tively. But since the loop as a whole is deflected to one side or the other, so that the cæcum goes either to the right iliac fossa (situs solitus) or to the left (situs inversus), there are four possible arrangements. These are (1) the normal,—situs solitus with dextral torsion, Fig. 12 *d*; (2) situs inversus with sinistral torsion, Fig. 12 *e*; (3) situs solitus with sinistral torsion, known as retroposition of the colon, since the colon crosses the small intestine dorsally, Fig. 12 *f*; and (4) which has apparently never been observed, situs inversus with dextral torsion, likewise causing retroposition of the colon, Fig. 12 *g*. Although situs inversus, partial or complete, is relatively common, retroposition of the colon (Fig. 12 *f*) is quite rare. Tscherning in 1883 reported a case in a laborer of 56 years who died of intestinal obstruction, and since then several others have been recorded.[22]

The cardiac loop also rotates dextrally, with rare sinistral exceptions, but the rotation is by no means as simple a process as the diagrams imply. Essential details in the development of the cardiac loop in the cat have been recorded by Schulte, whose work has been reviewed and supplemented in Murray's careful study of the rabbit.[23] The dextral torsion has the appearance of being carried beyond the limits of the heart itself, by the atrophy of left veins and right arteries in the originally bilateral series. Cases of sinistral torsion of the heart (situs inversus, Fig. 12 *b*) may similarly be intensified by the degeneration of *right* veins and *left* arteries, completely reversing the normal picture. But there is also a group of anomalies, included among the cases

[22] Tscherning, *Nordiskt med. Arkiv*, Bd. 15, No. 9, as cited with figures by Ekehorn, *Arch. f. klin. Chir.*, 1904, Bd. 72, p. 606. Strehl (*Arch. f. klin. Chir.*, 1908, Bd. 78, p. 13) presents an excellent figure of retroposition as found in a girl of 12 who died from the resulting obstruction. Cutore (*Anat. Anz.*, 1912, Bd. 40) in describing a case in an infant (figured on p. 385) refers (on p. 442) to previous records by Bastianelli (1904) and Righetti (1909). Hunter has recently recorded another case in an infant. *Brit. Med. Journ.*, 1922, II, p. 800–802.

[23] Schulte, *Amer. Journ. Anat.*, 1916, Vol. 20, p. 45–72. Murray, *ibid.*, 1919, Vol. 26, p. 29–39.

known as "transposition," in which the veins and arteries degenerate as is normal, though the cardiac loop has reversed its bend. Remak observed and figured a reversed bend in the heart of a young chick embryo,[24] and, with the writer, Dr. Abbott made reconstructions to picture what would happen if hearts with such an initial anomaly should continue their development.[25] Lochte had previously ascribed cases of corrected transposition to "an inversion of the cardiac loop."[26] Uncorrected transposition, we believe, may be due to partial or imperfect rotation, either dextral or sinistral.

The dextral rotation of the other organs is simpler, since no loops are involved. The stomach has long been described as rotating so that its left surface becomes ventral and its right surface dorsal, the entire organ shifting from the median plane to the left. This, however, is a complex process of unequal growth rather than simple rotation. As the stomach goes to the left, the liver turns to the right. The pancreas rotates in such a way that the right lobe of the ventral pancreas pursues the dorsal pancreas around the intestine to fuse with it, and the left lobe of ventral pancreas, if it does not atrophy or remain in situ to form an annular pancreas, may grow out under the gall-bladder. The trachea and œsophagus share in the dextral rotation, as is strikingly shown by Dr. C. Chang of Hopei University in a study now in progress. Finally there may be mentioned the dextral spiral trend of the muscle fibers throughout the digestive tube.[27]

Various causes have been assigned for this dextral rotation. Sometimes it has been attributed to the veins.

[24] Remak, R., "Untersuchungen über die Entwickelung der Wirbelthiere," 1851, Taf. III, Figs. 28, 29.

[25] This study has been only inadequately recorded—*Anat. Rec.*, 1915, Vol. 9, p. 103–105, together with brief references by Dr. Abbott in several publications.

[26] Lochte, "Ein Fall von Situs viscerum irregularis," *Beitr. z. path. Anat.*, 1898, Bd. 24, p. 187–222.

[27] Recently studied by Dr. Carey and Professor Sykes. *Cf. Science*, 1922, Vol. 55, p. 704–706.

"From our earlier investigations," wrote Lochte in 1898 (*l. c.*, p. 220–221), "we might assume that the normal position of the cardiac loop in situs solitus depended on the persistence of the left (*sic*) umbilical and omphalo-mesenteric veins." (The position of the stomach, duodenum and spleen he had likewise ascribed to the way in which the portal and umbilical veins develop.) "Without doubt in the normal formation of the cardiac loop these veins persist," he continues, "but it appears more than doubtful whether we are justified in recognizing a causal connection between the two: if one discards this hypothesis, the determining influence must reside in other factors which at present can not be more closely defined."

Three years after Lochte, the writer ventured the following opinion: "As the venous channels become predominant on the right side, the liver consequently develops more rapidly there and becomes a right-sided organ. Veins and liver combine to push the stomach to the left. . . . It may confidently be assumed that, had the originally symmetrical vessels persisted on the left side, stomach, liver, and later the vena cava would shift their position, resulting in situs inversus."

But these observations show merely the close correlation between the veins and the rotating organs, without locating the initiative—certainly it is not with the veins, predominant as they appear in sections. Papez in 1915, after a prolonged and careful embryological study, failed to find "a satisfactory mechanical explanation of intestinal rotation," but the influence of adjacent blood-vessels was considered eliminated. Rotation was ascribed to the growth of the epithelial tube. "The stomach swings boldly to the left and it appears that the intestine (*i.e.*, duodenum) is carried to the right by a compensatory bend of the elongating epithelial tube." "We are inclined to regard the gastric and intestinal bends together as forming an 'S,' comparable with S-shaped bends which soon develop in the mesentery itself."[28]

In what is perhaps the most recent study of "the mechanics of intestinal rotation," Vogt emphasizes the importance of this "alternating double coil" formed by the stomach and duodenum. The duodenum then turns back upon itself, pushing the mesentery to the left at the duodeno-jejunal flexure, and this flexure, according to

[28] Papez, J. W., *Anat. Rec.*, 1916, Vol. 10, p. 220–221; 1917, Vol. 11, p. 392–394.

Vogt, is "the key to the understanding of intestinal rotation."[29] In discussing Vogt's paper before the *Anatomische Gesellschaft,* Braus expressed some doubt as to the efficacy of the duodeno-jejunal flexure. Vogt utilizes it for intestinal rotation only, which is independent of that of the stomach. In the left-sided position of the stomach he recognized "one of the primary asymmetries which must be regarded as predetermined."

It seems evident that the attempt to select any vessel or organ as the cause of the spiral rotation is ill-advised, since in some anomaly, almost every "cause" may be shown clearly to be inoperative. The true motive is more pervasive and deep-seated than any of its early manifestations. In the thoroughgoing inversion of symmetry in the gastropod molluscs, Conklin finds that the reversal is evident with the first cleavage of the egg, and thinks that it may proceed from a reversal of polarity in the oocyte.[30] In mammals the initial inversion must arise much later, after the organs have developed, with apparently an indifferent bilateral symmetry. But the primary direction of the polarity of the ovum and the secondary rotation of bilateral organs, both tend to produce a great predominance of dextral spirals, and their presumably common cause lies in a field other than morphology. Here we have sought merely to show that all the principal viscera in man are disposed in accordance with a general dextral rotation, like that which prevails in the gastropod molluscs.

CONCLUSION

The examples which have been cited, inadequate as they may be, lead to the conclusion that nature is ill at ease—restless—in the presence of asymmetry. When a primary condition of symmetry has been lost, some new semblance of symmetry will be produced, and often

[29] Vogt, "Zur Morphologie und Mechanik der Darmdrehung," *Verh. d. anat. Gesel.,* 1920, p. 39–55.

[30] Conklin, E. G., "The Cause of Inverse Symmetry," *Anat. Anz.,* 1903, Bd. 23, p. 577–588.

a very perfect symmetry may be built upon the remains of that which has gone. Thus in plants we have seen that specific, generic, and even more far-reaching distinctions, may be evolved in this way. In mammals, a series of remarkable evolutionary changes, of little or no taxonomic value, have occurred in the aortic arches. If these are rightly interpreted on the basis of symmetry, further changes in the anatomy of man and mammals seem possible in a geological measure of time, and some seem so highly in accord with natural phenomena that the wonder is that they have not occurred already. Finally the spiral arrangement of the viscera in man, as superimposed upon, or derived from, bilateral symmetry, should be more comprehensively examined than heretofore, and must be reckoned with in connection with a wide range of anomalies, as well as in understanding normal anatomy.

Postscript. After the completion of this paper, Professor Conklin, in a notable course of Lowell Institute lectures, vigorously maintained that evolution must take place in the germ-cells, and especially in their chromosomes, to the exclusion of evolution in embryonic and later developmental stages, which it would be misleading to call "in the adult." It is difficult to see how this can be true of the floral variations and aortic patterns which have here been considered. That the future animal exists potentially and causally in the fertilized ovum seems proven by the subsequent course of events; yet to assume that the myriads of adult characters are there represented by particular genes or granules, through changes in which evolution is effected, implies a preformation far beyond the dreams of Hartsoeker and Dalenpatius, and subject to the same criticism which shattered them. A gene for so trivial a character as the iris-color should be accompanied by a hundred others for more important structural features of the eye, and thousands upon thousands, if all the bodily elements are similarly represented. The situation recalls Tyndall's train of thought when on the summit of the Matterhorn,—whether his pensiveness and the alpine peaks were potentially present in the earliest nebula!

From this incredible complexity we withdraw to a view in which epigenesis is recognized,—in which the body is not a by-product of the germ-plasm, and in which somatic changes play a large part in evolution. In the instance of the aortic arches, a somatic character, apparently acquired in embryos of some 10 mm., becomes an important feature in the evolution of various mammals. The now prevailing patterns in the pig and sheep, for example, presumably appeared in the ancestral animals as rare anomalies; these anomalies then became common; and finally, after they had become normal, these acquired characters could be called inherited. In the important instances here discussed, the cause of anomalies is the cause of evolution; and in these instances, typical of many others, it appears to be somatic rather than germinal.

TWO NEW COLOR FACTORS OF THE GUINEA PIG

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THE common laboratory rodents, the mouse, rat, guinea pig, and rabbit, were among the first animals to be studied genetically, following the rediscovery of Mendel's law. Some half dozen more or less closely parallel pairs of Mendelian factors, affecting color, were soon discovered in each case. Work with these animals has continued, but new independent pairs of factors have not been coming to light very rapidly. Instead, a considerable number of new factors have been discovered which have turned out to be allelomorphs of those already known. We thus have 3 allelomorphs in the hooded series in rats, 4 in the albino series of guinea pigs and also of rabbits, and 3 each in the albino series of rats and mice. Of agouti series allelomorphs, 4 are known in mice, 3 in rabbits and 3 in guinea pigs. There are 3 allelomorphs affecting density of black in rabbits and 3 in the tortoise-shell series of guinea pigs.[1]

One of the new factors of the guinea pig to be discussed here is of this kind, a fifth member of the albino series. The other has no known counterpart among rodents. Its closest parallel seems to be in certain imperfectly understood color variations among hogs.

The highest dominant (C) in the albino series of guinea pigs (Wright, 1915, 1916) is present in the ordinary intensely colored varieties showing black or red or both in the fur. Below this in dominance and order of effect is a grade of dilution of color (c^d) in which black is reduced

[1] A discussion of these multiple allelomorphic series with references to the original publications was given in a series of papers by the writer "Color Inheritance in Mammals," *Jour. Her.*, 8, 9, 1917, 1918. Since that time Castle (1921) has added a fourth member to the albino series of rabbits and Detlefsen (1921) has added a third to the albino series of mice. Other less clearly established cases have been suggested.

to a sepia color and red to yellow or cream. The eyes remain black. In the red-eyed dilutes with the next allelomorph (c^r) black is still represented by a sepia, darker even than in the previous case, but all red is eliminated from the coat. The red areas of tortoise shells and golden agoutis are replaced by white, giving us black and white guinea pigs with the tortoise shell instead of the piebald type of pattern, and silver agoutis. There is reason to believe that the intensification of sepia with c^r as compared with that found with c^d is due to the release of black pigment production from competition for some common element with the yellow-producing process (Wright, 1916–1917). Albinism (c^a) is the lowest member of the series. In guinea pigs complete albinism is not known except as the result of combinations of several factors which reduce pigment. The so-called guinea pig albinos have dark noses, ears and feet, and often sootiness on the back. As in the case of c^r, some black pigment is produced, but no yellow. The eyes are pink.

The intensity factor, C, is completely dominant over the others. Below this there is imperfect dominance. Where the homozygous dilutes c^dc^d have medium sepia and yellow, the heterozygotes c^dc^r and c^dc^a have dark sepia and cream, and light sepia and cream, respectively. The homozygote c^rc^r is almost black and white with very dark-red eyes, while c^rc^a is a light or medium sepia with light-red eyes.

On commencing investigation of the stocks of guinea pigs which had been maintained by the Bureau of Animal Industry, the writer found that intense types, dark-eyed dilutes, and albinos of the ordinary sooty kind were present. There were no red-eyed dilutes. All red-eyed dilutes in this country, probably, trace to a few animals brought from Peru in 1912 by Professor Castle (Castle, 1916). There were several inbred families which had been maintained by brother-sister mating since 1906, which the records indicated to be homozygous intense in

all lines living in 1916 (Families 2, 24, 31, 32, 34, 38 and 39). Others were found to be homozygous dilute in all lines at that time (14, 35 and 36). Both intense and dilute lines were present in three families (18, 20 and 23) and both intense and albino lines, or segregates, in three more (7, 13, and 17). One family (9) was predominantly dilute, but there were albino segregates.

Crosses soon made it clear that the dilution present in these families was allelomorphic with albinism, as in the case of that previously encountered by the writer in Professsor Castle's laboratory. Minor variations in intensity were found, however, which were not in the albino series. Family 32, for example, was characterized by a very intense red, family 38 by a light red, approaching yellow. The lines in family 18 which were not permanently intense red produced young much like family 38 at birth, but which became typical yellow later. Families 35 and 36 produced only young of a typical yellow. Crosses with albinos reduced the intensity of the red of family 32, but raised that of family 38. On the other hand, the yellow of both families 18 and 35 was reduced to the cream characteristic of dilutes heterozygous for albinism. It was thus clear that the marked difference in intensity between families 32 and 38 was not due to an albino series allelomorph. Both have factor C. Multiple independent modifying factors seem to be responsible for the difference in this and other cases of this kind. The first cross is intermediate, as is also F_2. No recognizable segregation has been observed. Similarly, the same dilution factor of the albino series seems to have been present in families 18 and 35 and all of the other dilute inbred families. We will not be concerned further in this paper with these minor variations in intensity, brought to light by inbreeding and lost on crossing.

While the dilutes of the inbred families were found to possess an allelomorph of albinism, there was a difference in appearance from the dilutes with which the writer had been familiar. There was much less dilution of the

black parts of the fur. The black in the homozygous dilutes was almost indistinguishable from that of intense guinea pigs, and those heterozygous for albinism were of a dark sepia color, never approaching the light sepia characteristic of Professor Castle's stock. On the other hand, the dilution of red (yellow in homozygous dilutes, cream in heterozygotes) was not conspicuously different from that in the latter stock.

This difference in color was made more evident by comparison with some dilutes which were kindly presented by Professor Castle. Knowing, however, that Professor Castle had especially selected for extreme dilution for several years (Castle, 1912) it was thought that the difference would probably turn out to be due to modifiers, as in his selection experiment with hooded rats (Castle, 1919). No special study of the variations in dilution was made at this time, but crosses were made with Professor Castle's dilutes for another purpose. During the course of the next two or three years it was noticed that typical light sepias occasionally segregated out among the descendants of these crosses. Experiments were then begun, to determine whether the difference was transmitted independently of albinism or not.

Light sepias, tracing to Professor Castle's dilute selection stock were mated with albinos of the Bureau stock, while dark sepias whose dilution factor came from families 9, 18 or 35 were mated with albino sons or daughters of light sepias. In the next and later generations, the dilutes from each type of mating were mated with albinos from the other.

If the difference in intensity were due to factors independent of the albino series, as suspected at first, it should be transmissible through albinos and the sepias from the two types of mating should be indistinguishable. In later generations, both dark and light sepias should segregate out of both if they did not merely blend together like the intense and light reds of families 32 and 38, previously discussed.

As it has turned, however, the two series have kept wholly distinct. The dark sepia of the Bureau line is as dark as ever and the light sepia tracing to Professor Castle's stock is as light as ever after as thorough a mixing of blood lines for several generations as is possible, through the albino parents. All young have been graded by standard sets of skins, the sepia set running from grade 3 for the lightest sepia to 14 for intense black and the yellow set running from grade 3 for the lightest cream to grade 13 for the red of family 32. The average grade in the dark series has been sepia 11.5, cream 4.6; in the light series, sepia 6.9 and cream 4.2. The lower limit of sepia in the dark series has been an occasional grade 10 and the upper limit in the light series a rare grade 9.

This result made it practically certain that a new allelomorph of albinism was involved. The symbol c^k has been adopted for this factor. The two types of mating may be represented as follows:

	Dark dilute	Light dilute	Albino
(1) $c^dc^a \times c^ac^a$ (from 2) $= c^dc^a + c^ac^a$	0	81	98
(2) $c^kc^a \times c^ac^a$ (from 1) $= c^kc^a + c^ac^a$	64	0	48

The existence of the new factor has been verified by production of all of the new compounds, c^kc^k, c^kc^d, c^kc^r, and c^kc^a, all thoroughly tested by matings with albinos and otherwise. The results have all been in conformity with the hypothesis, both qualitatively and quantitatively within the limits of random sampling.

All of these combinations have black eyes, as of course was to be expected. The homozygous dark dilutes c^kc^k have a very dark sepia, difficult to distinguish from blacks in some cases even by direct comparison, but a yellow averaging only slightly more intense than that of c^dc^d. The heterozygote between the two dilution factors, c^kc^d, is intermediate in color—a dark sepia and a typical yellow. The type c^kc^r is almost intense black, but with a typical cream, a striking combination. The heterozygotes with albinism c^kc^a are as described above, dark sepia and

cream. The five intense types, CC, Cc^k, Cc^d, Cc^r and Cc^a, have all been produced and tested. They are indistinguishable in appearance. Among the remaining 10 types, all are ordinarily distinguishable from each other if both sepia and yellow are present in the fur, except, curiously enough, the compounds c^kc^a and c^dc^r, which have no factor in common.

After finding this new member of the albino series, dilutes from all sources in the Bureau stock were tested for a possible sixth allelomorph. Yellows approaching red, and creams approaching yellow were found as well as some rather aberrant sepias. On mating with albinos from matings 1 and 2 above, these minor differences promptly disappeared in all but one case. With this one exception, all of these dilutes proved to have factor c^k or an allelomorph so close as to be indistinguishable. The exceptional case was from a mating (B211) in the random bred control stock, between an albino male and an intense golden agouti tricolor female. This control stock is the stock from which the various inbred families were wholly or in part derived and has been maintained with the careful avoidance of inbreeding. Little study had previously been made of its colors which had seemed to include nothing unusual. The above mating (B211) produced black-yellow and yellow agouti tricolors in addition to the ordinary intense black-red and golden agouti varieties. It seemed most likely that it was of the type $Cc^k \times c^ac^a$, but the dilute young showed a typical yellow (grade 7 or 8) in place of the cream (grade 4 or 5) usually found in c^kc^a, and a black of full intensity (grade 14) in place of dark sepia (grade 11 or 12). There were 11 young with red in the fur and 5 with yellow, in addition to an unclassifiable black—white bicolor. A mating between two of the dilute young produced six dilutes of their own type in addition to two albinos.

A dilute son and a dilute daughter of the original mating (B211) were mated with albinos from a type 1 mating in order to test for the suspected presence of a sixth

allelomorph. According to all past experience there should only have been dilute and albino young. The result, however, was 5 young with red in the fur, 5 intense blacks showing no red or yellow, and 17 albinos. A similar result was obtained from two dilutes from the mating between dilute progeny of B211 referred to above. These were mated with albinos of the ordinary stock and produced 9 intense young with red in the fur and 5 albinos, both happening to transmit the albino factor. These four matings of dilute by albino thus produced 20 intense young (14 showing intense red as well as intense black) in addition to 22 albinos.

This intensity must apparently have come from the albino parents in each case, since the new dilution was clearly recessive to the intensity of its own stock. An intensity factor transmitted by an albino could clearly not be the intensity factor (C) of the albino series. The symbol f has been adopted for the new dilution factor, and F for its dominant allelomorph.

The original mating, B211, was probably CCFf $\times$ $c^a c^a$Ff (11 intense; 5 dilute young). The matings of dilute progeny with ordinary albinos were of type Cc^aff $\times$ $c^a c^a$FF, giving intense young Cc^aFf in addition to albinos $c^a c^a$Ff.

Some of the intense young were back crossed to albinos of ordinary dilute stock. No dilute young appeared. There were 16 intense (8 showing red, 8 merely intense black) and 18 albinos. This, of course, is in harmony with the above hypothesis.

On the other hand, on crossing the F_1 young with their albino brothers or sisters, at least one dilute segregate of the new type was produced. These matings have produced 10 young showing red, 1 with yellow and 5 blacks, which could not, of course, be classified relative to the new dilution, and 14 albinos. A mating between two F_1 intense young, which should produce similar results, except for the proportion of albinos, has produced 1 young with red, 1 with yellow and 1 unclassifiable black.

Excluding the albinos and unclassifiable blacks, we have an F_2 ratio of 11 black-red intense to 2 black-yellow dilutes. As there is no intergrading of the red and yellow, there can be little doubt that a single recessive factor is involved.

Attempts have recently been made to combine this new dilution with that of the albino series. A mating between the two types ($Cc^aff \times c^kc^kFF$) resulted in 6 young with red (Cc^kFf) and 3 dark sepia-cream dilutes (c^kc^aFf).

Three matings between albinos known from their parentage to transmit the new dilution (c^ac^aFf) and ordinary dilutes (c^dc^aFF, c^kc^kFF) have resulted in 14 young like ordinary light or dark dilutes in appearance. The new black-yellow dilution was recovered in the next generation in the same litters as ordinary dilutes of the sepia-cream or sepia-yellow types.

One very interesting young one was produced by a mating known from the parentage of the dam and sire to be of the type $Cc^aFf \times Cc^dFf$. Among the young were a black-red (C—F—), a black-yellow (C—ff), a light sepia (c^dc^aF—) and a dark sepia-cream, several grades darker in its sepia (grade 13) than any heterozygous dilute of type c^dc^a ever graded before. A similar dark sepia has come from the mating $Cc^aff \times c^dc^aFf$. These anomalous dark sepias must apparently represent the desired combination of dilution factors c^dc^aff. If this is confirmed by the tests in progress it indicates that the new dilution factor intensifies black while diluting red. If we assume that its primary effect is the dilution of red the intensification of black can be explained as due to the partial release of the black producing process from competition with the process for producing red. The situation is somewhat comparable to the relation between factors c^d and c^r in the albino series, already referred to.

Animals with the new dilution factor have a typical yellow color when born. Later in life this changes to cream and in some cases, at least, it ultimately fades out altogether, leaving white. This is another contrast with

the effects of the dilution factors of the albino series. The yellows (c^kc^k, c^kc^d, c^dc^d) and the creams (c^kc^r, c^kc^a, c^dc^r, c^dc^a) have not been observed to change in intensity with the exception of the relatively slight change previously referred to in family 18. The black of the new dilutes remains intense. There is a gradual intensification of sepia in the dilutes of the albino series.

No factor with an effect of this kind has been described hitherto in rodents. No provision for it was made in the scheme for classification of mammalian color factors suggested by the writer in previous papers (Wright, 1916, 1917a). Certain color variations of the hog were, however, interpreted as due to dilution of red without any apparent dilution of black (Wright, 1918). A dominant factor of this kind seems to be present in Yorkshires (white) and Chester Whites in addition to a dominant factor which greatly restricts or eliminates black in the skin and bristles. It was also suggested that the black with white points of Berkshires and Poland Chinas represents a tortoise shell pattern of black and red (instead of piebald black and white as in Hampshires) in which red has been eliminated by specific dilution factors. This interpretation of the Berkshire and Poland China patterns has been confirmed in recent experiments by Detlefsen and Carmichael (Detlefsen and Carmichael, 1921).

It will thus be necessary to add a new class of color factors, specific diluters of red color, which will probably in general be found to have an intensifying effect on black.

Summary

A fifth member of the albino series of guinea pigs, dark dilution, c^k, has been identified. It causes distinctly less dilution of black pigment than does the previously known dilution factor c^d, although very little less dilution of red. It is recessive to intensity (C) but imperfectly dominant over light dilution (c^d), red eyed, non-yellow dilution (c^r) and albinism (c^a). The allelomorphic series, C, c^k, c^d, c^r, c^a, is the longest yet reported in mammals.

A factor (f) reducing red to a yellow, which fades later to cream and even white, but intensifying black, has been found among the descendants of a single mating. It behaves as a unit recessive to its normal allelomorph (F) and is transmitted independently of the albino series.

It is suggested that the intensification of black is a secondary consequence of a primary dilution of red and is due to a partial release from a competition between the processes of black and red color production, and is thus parallel to certain effects, previously described in the albino series.

This factor represents a new class of color factors in rodents. Its closest parallels seem to be found in certain color varieties of the hog.

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INHERITANCE IN DROSOPHILA HYDEI. I. WHITE AND VERMILION EYE-COLORS

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IN August, 1920, I collected locally a number of wild species of Drosophila, among them a large species with a spotted thorax which Doctor A. H. Sturtevant later identified for me as *hydei* (for a description of the species cf. Sturtevant, 1921). Stock cultures of the species were easily established and maintained in the usual way. The species was grown rather extensively and the cultures were examined closely for aberrant individuals. A number were found from time to time, but most of them failed to transmit their characteristics. Most of the deviations from type affected the wings, which are so frequently subject to somatic variations that the failure to establish them is not surprising.

One form which appeared in the stock cultures in September, 1920, proved to be a new genetic type. It is a form similar in appearance to "bobbed" in *melanogaster*. The dorso-central and scutellar bristles are reduced in size, and the markings on the abdomen may be either normal or of the scaly, irregularly-marked appearance which is exhibited by "bobbed" in *melanogaster*. The character is sex-limited, expressed only in females, and it reduces viability somewhat. Its mode of inheritance has not been determined. An attempt was made to establish a pure race by selection, but thus far it has not succeeded or the character is highly variable in expression. It is mentioned here because most of our stocks of *hydei* contained it at the time the experiments reported in this paper were performed, and its presence accounts for the discrepancies in the sex ratios exhibited by some cultures. Our locally-derived wild-type stock continually produces it, and our "bobbed" stocks still produce some

wild-type individuals. One wild-type stock, however, which we received from Doctor Sturtevant, a stock collected in the summer of 1920 in Alabama, is free from it. This stock has been carried under the designation, Stt.

White Eye-color

On March 9, 1922, a single white-eyed male was discovered in the wild-type stock. The eye-color of this male was pure white, identical in appearance with the corresponding character in *melanogaster*. No other white-eyed flies were discovered subsequently in the stock, although a number of females were tested separately to determine whether or not they were heterozygous for it.

The white-eyed male was mated to two females from the same stock, producing in culture no. 1, 178 wild-type females and 204 wild-type males. The same male was then mated to a female from the Stt stock, producing in culture no. 8, 121 females and 138 males, all wild-type. He was subsequently mated in culture no. 14 to four of his daughters from culture no. 1. Culture no. 14 produced 27 wild-type females, 57 wild-type males, 18 white females, and 69 white males. He was then mated in culture no. 29 to a wild-type daughter from culture no. 8. In culture no. 29 five sub-cultures were made at seven-day intervals, and these produced 151 wild-type females, 354 wild-type males, 129 white females and 298 white males. He was taken from culture no. 29 and mated in culture no. 97 to a wild-type female from culture no. 29. There were three sub-cultures under this culture number, which yielded 71 wild-type females, 195 wild-type males, 77 white females, and 223 white males. The complete history of the original white-eyed male has not yet been told. From culture no. 97 he was transferred with one of his daughters from the same culture to culture no. 111. This culture produced no flies. He was accidentally killed on June 7th while transferring him from one bottle to another. He lived 90 days in an incubator room maintained at 25° C. We have since found that this is not an unusual duration of life for males of this species.

White eye-color, symbol *w*, is clearly a recessive sex-linked character which exhibits exactly the same mode of inheritance as white eye-color in *melanogaster*. Various matings of white with wild-type have been made many times and have always been found to agree with expectation save for discrepancies in the sex ratio, due apparently to the presence of "bobbed," which reduces viability. These results are so elementary that it is not thought worth while to present the actual experimental data.

The white character exhibits no significant effect on viability. White flies of both sexes are fully fertile. In this respect they resemble white in *melanogaster* and differ from white in *obscura*, the females of which are reported by Lancefield (1922) to be sterile. Stocks of white have been established and maintained without any difficulty. A stock free from "bobbed" has been produced by repeated out-crossing to the Stt stock.

VERMILION EYE-COLOR

On March 29, 1922, an examination of the "bobbed" stock revealed the presence of seven males with a bright vermilion eye-color. Subsequently another bottle also produced vermilion segregants. Counts were made of the flies which emerged in this latter bottle. It produced 178 wild-type females and males and 34 vermilion males. The results probably indicate that one of the female parents of this stock culture was heterozygous for vermilion.

A number of matings were made of vermilion males with wild-type females from the same bottle. Of these only one, culture no. 22, produced anything but wild-type flies. It produced 35 wild-type females, 28 wild-type males, 34 vermilion females and 47 vermilion males. From this culture it was possible to establish a stock of vermilion flies, which, however, also exhibited the "bobbed" character.

Vermilion eye-color, symbol *v*, is, like white, a character of the first rank for genetic studies. The color is

almost exactly the same as that of vermilion in *melanogaster*. Since the wild-type eye-color of *hydei* is distinctly darker than that of *melanogaster*, the difference between vermilion and wild-type in the former is more marked than it is in the latter. In vermilion the ocelli are almost white, as they are in vermilion *melanogaster*, but they are not as distinctly white as those of white-eyed flies. Vermilion is a recessive sex-linked character which gives the usual results when crossed with wild-type. Numerous cultures have been counted of all matings of this type without observing a single deviation from expectation.

Linkage of White and Vermilion

Since white and vermilion are both sex-linked, they should, of course, exhibit linkage with each other. Moreover, since the characters are sex-linked, it is possible to secure linkage data without first establishing a double recessive race of white-vermilion flies. As a starting point, a white female was mated to a vermilion male. The F_1 progeny consisted of wild-type females and white males. In order to secure linkage data, F_1 wild-type females were mated singly to vermilion males. Any kind of male would have served the purpose of this test, but vermilion was chosen because of a desire to establish eventually a white-vermilion race. The results of the cultures are recorded in section A, Table I.

In order to obtain white-vermilion flies, a number of vermilion females from culture no. 85 were isolated and mated singly to white males. All of these cultures except one produced only wild-type females and vermilion males. The exception, culture no. 101, produced 70 wild-type females, 69 white females, 58 vermilion males and 61 white males. White-vermilion is indistinguishable from white, but the white males produced in this culture obviously must have been white-vermilion in composition. These white-vermilion males mated to wild-type females from the Stt stock produced wild-type females and males.

F_1 wild-type females from these cultures were mated singly with vermilion males in order to obtain recombination data. The results are recorded in section B, Table I.

TABLE I

Section A, P_1, white ♀ × vermilion ♂; BC, F_1 wild-type ♀♀ × vermilion ♂♂, singly. Section B, P_1, wild-type ♀ × white-vermilion ♂; BC, F_1 wild-type ♀♀ × vermilion ♂♂, singly.

Section A	Females		Males			Section B	Females		Males		
	+	v	v	w	+		+	v	+	w	v
85.....	64	84	84	82	7	143...	111	98	85	106	12
86.....	58	63	41	63	5	144...	91	84	114	101	5
87.....	100	74	66	75	6	145...	100	100	93	96	11
88.....	63	55	51	59	2	146...	74	69	83	86	13
89.....	94	95	84	84	4	147...	75	74	73	79	9
90.....	64	73	60	77	9	148...	64	57	67	66	10
92.....	82	79	57	96	9	149...	77	62	58	45	11
93.....	53	61	71	66	6	150...	48	43	34	47	2
94.....	140	129	117	133	9	151...	80	87	80	83	15
95.....	10	7	11	7	2	152...	87	90	105	95	14
Total....	728	720	642	742	59		807	764	792	804	102

In the determination of the percentage of recombinations from these data allowance must be made for our inability to separate white from white-vermilion. The simplest way to do this to multiply the visible recombination class, wild-type males in section A, and vermilion males in section B by two and divide by the total number of males. The females in these cultures obviously furnish no data on recombination. Applying this method to the data of section A, the recombination value from $\frac{w}{v}$ females is 8.2 per cent., and in section B from $\frac{w\ v}{}$ females, 12.0 per cent. The average value obtained by lumping the data together is 10.3 per cent. of recombinations.

The data may, however, be subjected to another form of treatment based on the inclusion in the white class of section A of white, parental, and white-vermilion, recombination, sub-classes; and in white of section B of the same sub-classes with reversed significances. If we

make use of the entire data and calculate the recombination percentages by application of the method of least squares, we obtain for section A, 10.0 per cent.; for section B, 8.6 per cent.; and for the totals from both sections, 9.3 per cent. of recombinations.

Discussion of Results

White and vermilion in *hydei* to all appearances correspond to the characters of the same names in *melanogaster*. It is, however, impossible to apply the direct test of crossing to demonstrate a parallelism between them because the two species will not hybridize. The recombination percentage of white and vermilion in *hydei*, 9.3 per cent., is distinctly lower than that reported by Morgan and Bridges (1916) for the corresponding loci in *melanogaster*, 30.5 per cent.; but it does agree closely with the map distance between white and vermilion in *obscura*, reported to be 8 units by Lancefield (1922), and that between yellow and vermilion in *virilis*, reported by the same author from data secured from Metz to be about 14 units. It is, of course, impossible to decide as yet what these differences signify, but their existence demonstrates the importance of pursuing parallel genetic studies among the various species of Drosophila.

Besides the characters described in this paper, Hyde, for whom the species was named, has discovered and studied two others: scarlet (1915) and an eye-character, called variable (1922). These two characters are both recessive autosomal characters. Hyde's (1922) data indicate that they belong to the same linkage group and exhibit about 25 per cent. of crossing-over. Sturtevant (1921) lists *hydei* as a species possessing a chromosome complex of type I of Metz (1916); *i.e.*, five large pairs of chromosomes of approximately equal size and one small pair. Six linkage groups, therefore, are to be expected, of which two have been demonstrated.

The possession of two excellent sex-linked characters paves the way for studies of non-disjunction in *hydei*.

We have not yet been able to establish a non-disjunction stock in the species, although numerous attempts have been made to secure exceptional individuals from crosses of wild-type with vermilion and white, and of vermilion with white. In one culture, no. 98, of wild-type ♀ with white ♂ a single exceptional white male was secured among 596 flies. He was successively mated to three females during the 76 days he lived; and sub-cultures were established at 7-day intervals during this period in order to provide the best possible conditions for the production of offspring. None of the matings, however, yielded any progeny. Apparently this male was an XO individual produced by primary non-disjunction in the female. If so, XO males in *hydei* are sterile, like those in *melanogaster*.

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A RED-SPOTTED SEX-LIMITED MUTATION IN BRUCHUS[1]

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IN the wild type of *Bruchus quadrimaculatus* which we have in our laboratory, the body color of both male and female is tan. This tan color the writer (1921)[2] described for it and its mutants (red, black and white) as belonging to the red (R) allelomorph body color series. Each mutant character is sex limited to a marked degree because every male for each mutant culture has tan elytra and body color instead of red, black or white elytra and body color, as their respective females have.

This paper concerns another sex-limited trait which is likewise somatically visible in the females but not in the males. In addition to the tan body color, the wild type of female has four black spots on her elytra, two on each elytrum, but the wild male has no spots on his elytra. This dimorphism is unique. On Sept. 22, 1921, the writer discovered in a culture pure for red (RR) a female having four red spots on her elytra instead of the usual four black spots. This female mutant was mated with a male from the same red culture from which she originated to determine if this new trait would breed true. Her progeny consisted of red spotted females and non-spotted males.

After several generations of selective breeding by mating virgin red-spotted females with males from this same stock, a culture pure for this trait was obtained. But as in the preceding case, there is complete dimor-

[1] Contribution from the Zoological Laboratory of the University of Oklahoma, Second Series No. 29.

[2] Breitenbecher, J. K., 1921, "The Genetic Evidence of a Multiple Allelomorph (Triple) System in Bruchus and its Relation to Sex-Limited Inheritance, *Genetics*, Vol. 6: 55–90.

phism, for homozygous males have no red spots nor any spots at all. One can not easily distinguish externally the males of the black-spotted cultures from the non-spotted males of the red-spotted homozygous stock. This relation is a sex-limited one because of two types of females and one kind of male. This is different from any other work reported as far as the writer is aware. We have records of sex-limited conditions where one type of male at least is similar to one of the female types or the converse. But in *Bruchus* the males carrying these genes are non-spotted, a condition not appearing in females.

THE BREEDING TESTS

By making a few preliminary tests it was discovered that the gene, red spots, is a complete dominant to black spots. The writer, therefore, used the symbols SS to designate red spots, and ss for the black ones. It was further discovered that these two contrasting characters were easier to distinguish in a culture pure for red body color (RRSS) carrying red spots and the second culture homozygous for red body (RRss) and black spots. An insect (RRSS) pure for red body and red spots showed upon examination that both were of the same degree of redness; however, these red spots were transferred to other factors of the R allelomorphs, so that red body and red spots are not caused by one factor, but by two which make an insect appear pure red except where the pattern in the female outlines the red spots. The same relation was again found for a black body color, and black spots (R_bR_bss) in the same individual are not determined by one gene but by two separate ones; even though the amount of pigment is often of the same degree. Cultures were also made pure for white bodies and black spots (R_wR_wrr). The wild stocks are always homozygous for tan bodies and black spots (rrss). The males, however, from any culture are always like the wild phenotype (tan, non-spotted).

Whenever a homozygous, red spotted (SS) female is

mated with a wild-type male, pure for black spots (ss), all progeny appear as red-spotted (Ss) females and wild-type (Ss) males. The F_1 offspring manifest a 1:1 sex-limited ratio, because the red spots in the males do not show, for the males never show spotting. The progeny from five such pairs are tabulated in Table I.

TABLE I

P_1 A Homozygous Red-spotted Female (SS) × A Wild-type Male Homozygous for black spots (ss)
F_1 as follows:

Pedigree Number of Each P_1 Pair	Females, Red Spotted (Ss)	Males, Wild Type [3] (Ss)
103	18	14
109	81	82
110	25	29
111	42	38
115	15	21
Totals	181	184
Calculated	182.5	182.5

TABLE II

RECIPROCAL CROSS

P_1 1 Black-spotted Female (ss), × 1 Wild-type Male (SS)
F_1 as follows:

Pedigree Number of Each P_1 Pair	Females Red Spotted (Ss)	Males Wild Type (Ss)
101	27	29
104	25	23
106	32	33
113	33	25
114	36	46
Totals	153	156
Calculated	154.5	154.5

The reciprocal cross with its data are collected in Table II. In this cross the female was homozygous for black spots (ss) and the wild-type male was pure for red spots (SS). The progeny from the five pairs mated gave females which were red spotted (Ss) and males of the

[3] Whenever the "Wild-type Male" is mentioned, it means that every male manifests a non-spotted phenotype for the pure cultures of the dominant factor, red spots, and its recessive allelomorph, black spots, and also for their hybrids.

wild non-spotted type, which were also actually heterozygous (Ss) for red spots. A 1:1 sex-limited ratio again appears as a result of this condition.

The results of both crosses demonstrate that the red spotted factor is a complete dominant to black spots. These allelomorphs are manifested both phenotypically and genotypically in the females, but only the latter in the males. It is evident that the F_1 progeny from both tests were heterozygous and consisted of all red-spotted (Ss) females and wild-type (Ss) males. Likewise when these pairs were mated their F_2 offspring, as tabulated in Table III, follow a 3:1:4 sex-limited ratio. The results of the seventeen pairs mated prove that there are three times as many red-spotted (SS, Ss, sS) as black-spotted (ss) females, and further that there are actually four (SS, Ss, sS, ss) possible combinations for the males, although they appear as one phenotype.

TABLE III

F_1 1 Red-spotted Female (Ss), × 1 Wild-type Male (Ss)
F_2 as follows:

Pedigree Number of Each F_1 Pair	Females		Males Wild Type (SS, Ss, sS, ss)
	Red Spotted (SS, Ss, sS)	Black Spotted (ss)	
111.1	29	10	24
111.2	23	10	33
111.3	29	9	49
111.5	22	5	40
113.1	23	7	31
113.2	35	10	64
113.8	17	5	39
113.10	24	8	35
114.1	46	16	77
114.2	30	8	29
114.4	35	9	37
114.5	29	10	36
114.6	22	8	22
114.7	18	7	23
115.1	32	10	41
115.2	45	14	73
115.3	10	7	19
Totals	468	153	642
Calculated	*459*	*153*	*612*

The next procedure consisted in carrying out the usual

back cross tests. The first one consisted in mating a F_1 red-spotted (Ss) female with a wild-type male, pure for black (ss) spots. The progeny from five pairs, shown in Table IV, consisted of red-spotted (Ss) females, black-spotted (ss) females, and wild-type (Ss, ss) males. These phenotypes manifested a 1:1:2 sex-limited ratio. Of the two kinds of males, however, half were actually heterozygous for red spots and black ones and half homozygous for black spots.

TABLE IV

BACK CROSS TEST

P_1 1 Red-spotted Female (Ss), × 1 Wild-type Male (ss)
F_1 as follows:

Pedigree Number of the P_1 Pair	Females		Males Wild Type (Ss, ss)
	Red Spotted (Ss)	Black Spotted (ss)	
101.1	16	19	36
101.2	19	16	31
109.8	13	11	29
109.9	5	3	8
109.11	15	18	34
Totals	68	67	138
Calculated	*68*	*68*	*132*

The second back cross test was the reciprocal of the previous one. The female was homozygous for black spots (ss), while the F_1 male (Ss) appeared normal even though it was heterozygous for red spots and black ones. The offspring from five pairs are given in Table V, and the same result is evident as enumerated for Table IV. There were likewise two kinds of females, red spotted (Ss) and black spotted (ss) ones, while the males were as usual of the wild type but carried two sets of factors (Ss, ss). These three different phenotypes manifest again a 1:1:2 sex-limited ratio.

The third back cross test consisted in mating an F_1 red spotted (Ss) female with a wild-type male homozygous for (SS). The five pairs mated again gave a 1:1 sex-limited ratio for their offspring. Table VI shows that

TABLE V

BACK CROSS TEST

Reciprocal Cross

P_1 1 Black-spotted Female (ss), × 1 Wild-type Male (Ss)
F_1 as follows:

Pedigree Number of the P_1 Pairs	Females		Males Wild Type (Ss, ss)
	Red Spotted (Ss)	Black Spotted (ss)	
106.2	8	9	19
106.3	9	10	20
106.4	15	14	33
106.5	20	21	40
106.6	29	26	51
Totals	81	80	163
Calculated	*81*	*81*	*162*

the females were all red spotted (SS, Ss) and every male was of the wild type but carried the same factors (SS, Ss) as the females.

TABLE VI

BACK CROSS TEST

P_1 1 Red-spotted Female (Ss), × 1 Wild-type Male (SS)
F_1 as follows:

Pedigree Number of Each P_1 Pair	Females Red Spotted (SS, Ss)	Males Wild Type (S^s, Ss)
106.1	18	19
106.10	29	33
106.11	19	16
118.9	43	41
118.8	35	30
Totals	134	139
Calculated	136.5	136.5

The final back cross test was the reciprocal of the one just described, a pure red-spotted (SS) female being mated to a heterozygous (Ss) F_1 wild-type male. The total offspring from five such pairs approximate again a 1:1 sex-limited ratio (Table VII) because all the females were red spotted (SS, Ss) and the males were again of the non-spotted wild type, but carried the identical genes (SS, Ss) as their respective females.

TABLE VII

BACK CROSS TEST

Reciprocal Cross

P_1 1 Red-spotted Female (SS), × 1 Wild-type Male (Ss)
F_1 as follows:

Pedigree number of each F_1 pair	Females Red Spotted (SS, Ss)	Males Wild Type (SS, Ss)
100.1	23	24
100.2	32	30
100.3	41	45
100.4	39	42
100.5	27	23
Totals	162	164
Calculated	163	163

CONCLUSIONS

In our cultures of *Bruchus quadrimaculatus,* the so-called "four-spotted cowpea-weevil," the wild insects have a tan body and elytra color for both male and female and, further, every female of such stocks has four black spots, two on each elytrum, but the males are non-spotted.

In a culture pure for red body and elytra was found a female having four red on her elytra instead of the usual four black spots. This unusual type proved to be the result of a mutation from black spots to red spots. Pure cultures of this red-spotted mutation showed the same degree of sex limitation as the black spotted wild type, because its males were likewise non-spotted.

Lastly, the gene for red spots is a complete dominant to the black-spotted factor. Here also is further evidence that dominant mutations are not uncommon in *Bruchus* because the three mutations described previously and the one in this paper are complete Mendelian dominants.

A SIMPLE FORMULA GIVING THE NUMBER OF INDIVIDUALS REQUIRED FOR OBTAINING ONE OF A GIVEN FREQUENCY

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IT often happens in genetic work that a cross is made for the purpose of producing—or testing the possibility of producing—a particular type of individual, when a given frequency of occurrence of such individuals is expected on the basis of certain *a priori* considerations. Thus, let us say that it is expected theoretically that one among sixty-four of the progeny may be of the desired type. The question then arises, how many individuals should we prepare to raise in order to be sure of securing at least one of the kind sought for—provided our theoretical expectation is correct. An extremely simple calculation gives the answer, after we have defined the word "sure"—which otherwise is inexact, since there is no such thing as perfect certainty. If we define sure as meaning 99 chances of success to one of failure—*i.e.*, a chance of failure (F) of only .01—then we must raise 4.6 times $63\frac{1}{2}$ individuals (or 292) to be "sure" of getting the special one sought for. And in case such an individual then fails to appear, it will be "proved" (made highly probable) that the theory that gave the expectation one in 64 is incorrect. If, to take another example, we were looking for a particular crossover combination that we expected just once among each thousand offspring, we must prepare to get $4.6 \times 999\frac{1}{2}$, or 4598 offspring, to be similarly sure of securing one of these crossover individuals.

Even where a large proportion of the "desired" individuals are expected, such as one among every two or three of the total number, the question raised above still

[1] Department of Zoology, Contribution no. 160.

remains important in those cases in which the individuals cannot be classified by inspection alone but must be tested to determine their composition. For then our formula will tell us the minimum number of individuals which it is necessary to test, in order to be sure to include one of the kind desired. Thus, for instance, suppose we wished to inbreed a homozygous dominant derived from an F_2 plant population of the type 1AA : 2Aa : 1aa; how many individuals of the dominant type must we inbreed in order to be sure that we are including one homozygote? Since one among every 3 dominants is of the required homozygous kind, the number that must be bred is, according to our previous method of calculation, $4.6 \times 2\frac{1}{2}$, or 11.5 (12 to be safe). Or if a back cross had been made, giving a ratio of one heterozygous to one homozygous dominant indistinguishable from each other (one heterozygote among every two individuals), we should have to test $4.6 \times 1\frac{1}{2}$, or 7 individuals, to be sure that we were breeding from at least one heterozygote (or homozygote).

The number 4.6 is the (negative of the) natural logarithm ($\log_e$) of .01, the chance of our failing to get any individuals of the desired kind; it may be found either by looking it up directly in a table of natural logarithms or else by looking up the common logarithm ($\log_{10}$) in an ordinary logarithm table, and multiplying its numerical value (in this case 2.00) by 2.30, the coefficient which converts common to natural logarithms. If, now, our standard of certainty were lower, so that we were satisfied with a chance of success of nine out of ten—or a chance of failure (F) of .1 instead of .01—we should have to use the (negative of the) natural logarithm of .1, which is 2.3, instead of 4.6. In that case n, the number of offspring to be raised, in the first example above would have been $2.3 \times 63\frac{1}{2}$, or 146; in the second example n would have been $2.3 \times 999\frac{1}{2}$, or 2399; in the third example n would have been 5, and in the fourth between 3 and 4.

We may sum up all of this in the formula:

$$n = -\log_e F(P - \tfrac{1}{2}), \qquad (1)$$

where P is the expected number, such as 64, 1000, 3 and 2, respectively, which on the average will include one individual of the "desired" type. (It will be observed that P is the reciprocal of the chance that any one individual shall be of such type; the latter chance is usually designated as p, so that $P = 1/p$.) As any one investigator commonly tries to retain the same standard of certainty (or "chance of failure," F) throughout most of his experiments, it will only be necessary for him to remember the one number for $-\log_e F$ (such as 4.6); he may then multiply this same number by whatever $P - \frac{1}{2}$ he is dealing with, and so obtain n directly, without recourse to logarithmic or other tables, or to any calculations.

The above formula is also useful in a somewhat different connection. Sometimes the cross has been already performed, or the number involved can not be exactly controlled, so that n is given. If no individuals of the type in question have appeared among this number, the problem is then raised, has our theoretical P (or p) been disproved by the results or not; *i.e.*, what was the chance (F) of this failure to obtain any "desired" individuals, on the supposition that our P had been correct? Here, then, n and P are given, and F is to be found. From formula (1) we find that

$$\log_e F = -\frac{n}{P - \frac{1}{2}} \qquad (2)$$

Having thus found $\log_e F$, we may look up F itself in a logarithm table. In terms of common logarithms we have:

$$\log_{10} F = -\frac{n}{2.3(P - \frac{1}{2})}.$$

As an example, we may imagine that a group of 60 F_2 has been counted, and that all these are of the dominant type. Certain theoretical considerations may have led us to expect that either a ratio of 15 dominants: 1 recessive ($P = 16$) or all dominants would obtain. We may then ask, do the results disprove the 15:1 interpretation,

i.e., just what would have been the likelihood of getting this result if P had been 16. This likelihood is what we have called F, and by our formula

$$\log_{10} F = -\frac{60}{2.3 \times 15\frac{1}{2}} = -1.683.$$

For use in a logarithm table this number is then changed to the form $-2 + .317$. We now find in a table of common logarithms that $F = .02075$. Hence there was only .02 chance, or one chance in 50, of getting no recessives among the 60 F_2 if P had been 16, and, other considerations being equal, we must regard the 1:0 interpretation as being far more probable than that of 15:1.

It may be noted that in cases where $\log_{10} F$ turns out to be less than -2, it will usually be unnecessary to look up its value in a logarithm table, for in such cases F must have a value of less than .01, and we can therefore take it for granted without further calculation that the P assumed in the formula was incorrect. Conversely, when $\log_{10} F$ turns out to be greater than -1, we know that F must have been greater than .1, and that the assumed P was therefore quite possible. Use of a logarithm table will seldom be required, then, except when $\log_{10} F$ turns out to be between -1 and -2, and here a small table, containing only 10 values, would ordinarily be quite sufficient to give us the information concerning the probability which is needed.

Blakeslee, Belling, and Harris[2] have recently published tables showing the value of F for all practically possible values of n in the case of seven different values of P,—2, 3, 4, 6, 9, 12 and 36, respectively. When P has these values, therefore, these tables may be used in place of formula (2) and logarithm tables, for finding F (n being given). For finding n, however (F given), formula (1) will be easier to use than any tables, in the ordinary cases where F has a certain standard value, the log of which may be remembered.

[2] Blakeslee, A. F., Belling, J., and Harris, J. A., "The Probability Established by a Culture of Given Size that a Mating is Capable of Producing only Dominant Individuals," AMERICAN NATURALIST, Vol. 56, pp. 458–461; Sept.–Oct., 1922.

The formula given is only an approximation; a closer approximation is:

$$n = -\log_e F(P - .51). \qquad (3)$$

As will be shown presently, however, the number of individuals (n) as calculated by formula (1) never differs from the true value by as much as half of a single individual, and in all ordinary cases the error is much less even than this; hence, since we cannot deal with fractions of individuals, the number obtained is quite correct for our purpose. In finding F, where even less exactness is required, the error is likewise entirely negligible.

We may now give the proof of our formula. Let $1/P = p$, the chance that any one individual shall be of the desired type. Then the chance that any individual shall be of the other (more usual) type is $1 - p$, and F, the chance that all n individuals shall be of the usual type, must be $(1 - p)^n$. Taking the log of $F = (1 - p)^n$, we obtain the formula $\log F = n \log (1 - p)$ or

$$n = \frac{\log F}{\log(1 - p)}.$$

This is the strictly accurate formula, which is, of course, well known. It may, however, also be written in the form

$$n = -\log_e F(P - \tfrac{1}{2}) \times \frac{-1}{(P - \tfrac{1}{2}) \log_e (1 - p)} \qquad (4)$$

(by merely multiplying both numerator and denominator of the expression on the right hand by $-(P - \frac{1}{2})$).

Let us call the true n, found by the accurate formula given above, n_t, and the approximate n (found by formula 1), n_a. Then it is evident from (4) that

$$n_t = n_a \times \frac{-1}{(P - \tfrac{1}{2}) \log_e (1 - p)}.$$

In order to prove, then, that our approximation formula gives nearly correct results, we may prove that, for all values of P which would be used in practice, the factor $-1/(P - \frac{1}{2}) \log_e (1 - p)$ is so nearly equal to 1 that it may be neglected.

Table I shows (in column A) the values of this factor,

TABLE I

Mendelian Ratio	*A* $\frac{-1}{(P-\frac{1}{2})\log_e(1-p)}$	*B* Error, in %	*C* Absolute Error of n_a	*D* Absolute Error of n_a when $F=.001$
1 : 1	.961	3.9 %	$.06-\times-\log_e F$	.39
2 : 1	.987	1.3%	$.03+\times-\log_e F$	.23
3 : 1	.993	0.7 %	$.02+\times-\log_e F$	.17
7 : 1	.9985	0.15%	$.01+\times-\log_e F$	.08
15 : 1	.9996	0.04%	$.01-\times-\log_e F$	.04
31 : 1	.9998	0.02%	$.01-\times-\log_e F$	.04
63 : 1	.9999	0.01%	$.01-\times-\log_e F$	.05(±)

for a number of the commoner Mendelian ratios, together with (column *B*) the percentage[3] deviation of the factor from 1. It will be seen that the percentage difference between the factor $-1/(P-\frac{1}{2})\log_e(1-p)$ and 1 is only 3.9 per cent. for the lowest values of P, and decreases as P increases. Since, in finding n_t, this factor is merely multiplied by n_a, it is evident that the percentage deviation of the factor from 1 is the same as the percentage deviation of n_t from n_a—*i.e.*, the percentage error of n_a. The absolute error in the final result would of course be this percentage $\times$ n_a itself, and this absolute error has also been listed in the table (column *C*) in terms of multiples of $-\log_e F$, since the latter may be different in different cases. In practice (when n is to be found) $-\log_e F$ would hardly ever have a greater numerical value than 6.9, as this corresponds with a chance of success of 999:1. In that case, as will be seen from column *D*, the absolute error for the 1:1 ratio—the greatest error of all—would be only $.06 \times 6.9$, or .4 of one individual, and the absolute error in most of the other cases would be less than .1 of an individual, no matter how big n itself became. For more usual values of $\log_e F$ the absolute error would be still smaller.

It can be shown algebraically that as P increases (*i.e.*, as p approaches 0) the value of the factor $-1/(P-\frac{1}{2})\log_e(1-p)$ approaches 1 as a limit (and that therefore the approximation formula gives results having a smaller

[3] Per cent. taken on the basis of the assumed (approximation) value.

and smaller percentage error as P increases). The proof is as follows:

$$\lim_{p\to 0} \frac{-1}{(P-\frac{1}{2})\log_e(1-p)} = \lim_{p\to 0} \frac{-1}{\left(\frac{1}{p}-\frac{1}{2}\right)\log_e(1-p)}$$

$$= \lim_{p\to 0} \frac{-1}{\frac{2-p}{2p}\log_e(1-p)} = \lim_{p\to 0} \frac{-2p}{(2-p)\log_e(1-p)}.$$

To evaluate the limit of the latter expression, we may first take the derivatives of the numerator and denominator (since the limit of a quotient equals the limit of the quotient of the derivative of the numerator divided by the derivative of the denominator). Thus we find:

$$= \lim_{p\to 0} \frac{-2}{(2-p)\frac{-1}{1-p} - \log_e(1-p)}.$$

$$\text{(Substituting 0 for } p) = \frac{-2}{2(-1)-0} = \frac{-2}{-2} = 1.$$

$$\text{Wherefore, } \lim_{p\to 0} \frac{-1}{(P-\frac{1}{2})\log_e(1-p)} = 1.$$

Table II is constructed similarly to Table I, but gives the results for the more accurate approximation formula $n = -\log_e F(P-.51)$. It will be seen that little is gained by using the more accurate formula. The approach of the factor $-1/(P-.51)\log_e(1-p)$ to the

TABLE II

Mendelian Ratio	A $\frac{-1}{(P-.51)\log_e(1-p)}$	B Error, in %	C Absolute Error of n_a	D Absolute Error of n_a when $F=.001$
1 : 1	.967	3.3%	$.05-\times-\log_e F$	.33
2 : 1	.991	0.9%	$.02+\times-\log_e F$	.16
3 : 1	.996	0.4%	$.01+\times-\log_e F$	.10
7 : 1	.9999	0.01%	$.00+\times-\log_e F$	.01
15 : 1	1.0003	−0.03%	$.00-\times-\log_e F$	−.03
31 : 1	1.0001	−0.01%	$.00-\times-\log_e F$	−.03
63 : 1	1.00003	−0.003%	$.00-\times-\log_e F$	−.01

limit 1, as P increases, and the consequent greater and greater accuracy of this approximation formula, for higher and higher values of P, may be proved by a method similar to that used for the other formula.

In the attempt to find the approximation formulæ, the limiting value of n/P, as P grew indefinitely large, was first found,—starting with the equation

$$n = \frac{\log F}{\log (1 - p)}.$$

The limiting value proved to be $\log_e F$ itself. For this evaluation I am indebted to Dr. J. M. Jacobs, of the Department of Mathematics of the University of Texas.

It was then found that when this limiting value, $\log_e F$, was equated to n/P, and the equation (in the form $n = P \log_e F$) used as an approximation for finding n in the case of small values of P, the errors varied with a regularity such that they could be largely eliminated by substituting $P - .51$ for P itself in the formula. $\text{Log}_e F$ was then seen to be the limiting value of $n/(P - .51)$ also; in fact, any constant may be substituted for .51 and the expression will still have the limiting value $\log_e F$ as P grows indefinitely large, but it was found that .51 is the constant which gives the most nearly correct results for smaller values of P.

Summary

A short approximation formula (see (2)) has been found for estimating the probability of a given expected ratio having been correct, when no individuals of the minority type have appeared. In using the formula for this purpose, it will in some cases be necessary to look up one logarithm, but no other tables and very little calculation are required. The same formula may also be used (in form (1)) to determine the number of individuals that must be raised and classified (by inspection or testing) in order to be sure of finding one of a theoretically given frequency. The calculation for the latter purpose ordinarily consists of only a simple multiplication, without the use of any tables.

FAMILY RESEMBLANCES AMONG AMERICAN MEN OF SCIENCE

II. Degree of Resemblance in Comparison with the Generality: Proportion of Workers in Each Science and Distribution of Replies

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The methods used in determining the number of workers in the various fields of science resulted in distributing the thousand as recorded in the first column of the table below. The second column shows the number of replies from those in the several divisions, of whom, owing to two selections of the group, there were 1,154.

TABLE I

Science	1	2
Astronomy	50	44
Chemistry	175	167
Geology	100	90
Mathematics	80	76
Physics	150	161
Anatomy	25	23
Anthropology	20	18
Botany	100	97
Pathology	60	56
Physiology	40	37
Psychology	50	43
Zoology	150	144
Total	1,000	956

It is obvious without expressing the replies in ratios per one thousand that they are evenly distributed, the only variation in any way unusual being those in the physics group, and the relatively large number makes that difference of little consequence.

Resemblance in Distinction Compared with the Generality

Two hundred and fifty-six, or more than one in four of those reporting, are known to have distinguished relatives

no more remote in relationship than cousin. Table I has given the facts concerning the distribution of replies, showing the evenness of the selection. Table II gives the facts concerning the distribution of those replying and the numbers with distinguished relatives.

TABLE II

Science	(1) Number Reporting	(2) Number Known to have Distinguished Relatives	(3) Column (2) Reduced to Number per 1,000	(4) Number of Distinguished Relatives	(5) Number of Distinguished Relatives per 1,000
Astronomy	44	10	227	17	386
Chemistry	167	43	257	96	575
Geology	90	35	389	65	722
Mathematics	76	14	184	28	368
Physics	161	38	236	82	509
Anatomy	23	7	304	11	478
Anthropology	18	3	167	5	278
Botany	97	22	227	36	371
Pathology	56	21	375	39	696
Physiology	37	8	216	20	541
Psychology	43	16	372	28	651
Zoology	144	39	271	71	493
Total	956	256	267.8 ± 14	498	521

It will be seen that 44 astronomers replied, and that 10 were found to have one or more distinguished relatives of a degree no more remote than cousin. This means that for 1,000 astronomers there would be 227 with distinguished relatives. Of 1,000 chemists 257 would have distinguished relatives, as defined. The average for the twelve groups is shown to be 267.8 with a p.e. of 14. The number of relatives per thousand men reporting is given in the last column. Forty-four astronomers are represented by 386 persons of distinction; 167 chemists by 575 persons of distinction; geology by 722; mathematics by 368, and so on. The average for this set of values is 521. Two hundred and fifty-six men of science have 498 relatives as defined; this is practically two per man. The exact value per man being $1.95 \pm .06$, using the following values for the twelve sciences as the distribution for which the p.e. is obtained: The number per

man for astronomy is 1.7; for chemistry 2.2; for geology 2.1; mathematics 2.0; physics 2.2; anatomy 1.6; anthropology 1.7; botany 1.6; pathology 1.9; physiology 2.5; psychology 2.5, and zoology 1.8.

TABLE III

DISTRIBUTION OF THE BIOGRAPHIES IN "AMERICAN MEN OF SCIENCE," "WHO'S WHO IN AMERICA" AND "APPLETON'S CYCLOPEDIA OF AMERICAN BIOGRAPHY," AND THE STARRED GROUP OF "AMERICAN MEN OF SCIENCE," ACCORDING TO NUMBER IN EACH DEGREE OF RELATIONSHIP.

	Total in All Three Books	Distribution in the Three Hand-books and in the Starred Group			
		A	W	E	X
B	146	62	121	18	26
Si	13	2	13		
S	18	15	13		5
D	1		1		
F	78	17	40	52	5
M	3		2	2	
FB	33	1	13	26	
FSi	4		3	3	
MB	31	1	11	25	1
MSi					
BS	6	5	5		
BD	3		3		
SiS	3	2	3		1
SiD					
FF	17			17	
FM	1			1	
MF	35		2	35	
MM	1			1	
FBS	45	15	37	7	9
FBD					
FSiS	15	4	13	2	3
FSiD	2		2		
MBS	20	7	18	6	4
MBD	1		1		
MSiS	18	7	16	3	4
MSiD	4	1	4		
Total	498	139	321	198	58

A denotes "American Men of Science."
W denotes "Who's Who in America."
E denotes "Appleton's Cyclopedia of American Biography."
X denotes members of the 'starred' group in "American Men of Science."

At first sight it might seem that the mathematical sciences had a definitely greater number of relatives per man than the more descriptive and biological sciences.

The exceptions in the case of astronomy, physiology and psychology discount the evidence in the other cases. It is likely that a careful analysis of the relation between the number of men reporting relatives and the number of relatives per man would reveal facts of significance. As the figures stand, it seems best to accept them as chance variations.

The range of selection in time and people covered by three handbooks used to determine distinction of those found makes direct comparisons of the totals in Table II less clear than is desirable.

Table III gives the distribution of the 498 relatives listed in Table II and shows (1) the number in each degree of relationship, (2) the number in each one of the three handbooks and the number in the starred group. Thus, there are 146 brothers found in one or more of the three handbooks. Of these, 62 are in American Men of Science, 121 are in "Who's Who in America" and 18 are in "Appleton's Cyclopedia of American Biography." Of the 62 in "American Men of Science" 26 are in the starred group. The significance of Table III lies mainly in the simple way it expresses some of the complicated results of the study. It is an appropriate introduction to the detailed Table IV which follows the account of the duplications in relationship.

"Duplicated" Relatives

It is well to call attention to the fact that the word relationships might better be used than relatives. It is quite correct to say that 956 men are known to have 146 distinguished brothers, although six of these brothers are counted twice as brothers and seven are counted again as cousins of 146 distinguished brothers. It may seem illogical to count such cases twice, yet no better treatment is evident. The fact remains that if we consider each person in our group as an individual, there are 146 brothers of these several individuals. If the six repetitions in the brother relationship are to be eliminated, which brother is to be deprived of a relative? The total

known repetitions are 31; less than 6.5 per cent. of the 498 relationships.

TABLE IV

	Distribution of Those Distinguished in Science										Distribution of Those Not Distinguished in Science				Total for Both Groups
	A	W(S)	E(S)	AW	WE	XA	XAW	AWE	XAWE	Total in Science	W	E	WE	Total not in Science	
B	18	10	3	15		1	21	3	4	75	63	3	5	71	146
Si		2		2						4	9			9	13
S	5	2		5			5			17	1			1	18
D											1			1	1
F	3	1	14	3	1		2	6	3	33	17	21	7	45	78
M											1	1	1	3	3
FB			6	1						7	6	14	6	26	33
FSi											1	1	2	4	4
MB			7		1				1	9	6	13	3	22	31
MSi															
BS	1			4						5	1			1	6
BD											3			3	3
SiS				1			1			2	1			1	3
SiD															
FF			3							3		14		14	17
FM												1		1	1
MF			10							10		23	2	25	35
MM												1		1	1
FBS	3	4	2	3			9			21	19	3	2	24	45
FBD															
FSiS	1	1					2		1	5	9	1		10	15
FSiD											2			2	2
MBS		2	1	3			2		2	10	7	1	2	10	20
MBD		1								1					1
MSiS	1	2		2			3		1	9	7	1	1	9	18
MSiD										1	3			3	4
Total	32	25	46	40	2	1	45	9	12	212	157	98	31	286	498

Here is shown the distribution of the relatives (1) according to the number in each degree of kinship, (2) according to the number of handbooks in which the biographies are found, (3) the number in the starred group, (4) the number distinguished in science, (5) the number not distinguished in science, although eminent in some other activity than science. In column two under A,

we have the number 18. This means that 18 brothers are listed in "American Men of Science" and in no other handbook. W(S) indicates that 10 brothers who were distinguished in science were listed in "Who's Who in America" but in no other handbook. The E(S) means the same for Appleton's "Cyclopedia of American Biography." The other combinations mean that the individual is in the starred group (marked X) and the books represented by the letters. Thus, in vertical column under XAWE, we have listed the relatives who belong to the starred group and who are mentioned in all three handbooks. The column of totals beginning with 75 gives the number in each degree of kinship who are distinguished in science. The next section to the right gives the same sort of distribution for the biographies of those shown not to be distinguished in science.

All persons counted as belonging to the "science" group have been indicated in the lists by having their names printed in small capitals. Inclusion in "American Men of Science," membership in scientific societies with "performance" qualifications, teaching position in science, university degrees from departments of science, were the criteria on which most of the persons were counted as belonging to the group distinguished for performance in science. Some few, especially those whose records were found only in Appleton's Cyclopedia, were counted as scientific if the descriptive accounts were judged to warrant such inclusion. Where individuals were distinguished in science and other fields as well, they were counted in the first group. A more detailed analysis of the problem of specialization of resemblance is given in a following chapter.

Comparison of the Brothers with the Brothers of the Generality

It has been found desirable in the interest of simplicity and accuracy to compare part of the group of brothers listed in "Who's Who in America" with men of the generality. These brothers are those found listed in Vol. 7

(1912–13). The advantages of such a limitation are (1) that the selection is general, that is, it is not limited to one field of activity but is supposed to cover all fields with a measure which includes people of approximately the same minimum grade, (2) the number of living notables in the book may be compared with the generality, and more particularly the number of the same age limits, (3) this volume covers very nearly the exact period at which requests were being answered by the members of the group studied.

Table V gives the distribution of brothers selected in this manner and arranged according to the scientific activity of the men whose brothers they are, also according to the number who have worked in science and the number who have not.

TABLE V

DISTRIBUTION OF BIOGRAPHIES OF BROTHERS IN VOL. 7, 1912–13, WHO'S WHO IN AMERICA

Science	Number Reporting	Number of Brothers Found Listed in Vol. 7 of W. W. in A.	Number in Science	Number Not in Science
Astronomy	44	5	3	2
Chemistry	167	16	8	8
Geology	90	14	6	8
Mathematics	76	5		5
Physics	161	20	13	7
Anatomy	23	1		1
Anthropology	18	3	1	2
Botany	97	8	5	3
Pathology	56	8	4	4
Physiology	37	2		2
Psychology	43	9	1	8
Zoology	144	15	6	9
Total	956	106	47	59

Table V shows that 956 men of science have 106 brothers listed in the particular volume chosen. This volume has a total of 18,794 sketches of which approximately nine per cent., or 1,700, are women. Thus, there are 17,000 of the generality of 1911 who are comparable with 106 brothers of men of science.

The average age at which men become mentioned for the first time in "Who's Who in America" was determined for volume six, and found to be 49.9 years. It would not be far different for the years covered by the next volume. The average age of men of the starred group at the time of the second selection was 48.12 years. In 1911, the time at which the replies to the requests were being received, the men themselves and their brothers would have almost reached this average age at which men are included. The brothers of the men of the starred group are, thus, rather nicely comparable with those included in volume 7 of "Who's Who in America," so far as age limits are concerned.

The selection of a number of men of the generality comparable with the 956 men of science is not so simple. The most reasonable method seems to be that of determining the number of males of the total population in 1911 above the median age at which they first attain a place in the handbook, then adding a like number from the total of the male population below this point. Use of this method gives a total of approximately 14,000,000 males for the group who are comparable with men in "Who's Who in America" and the men of science.

There are approximately 17,000 men of the "Who's-Who-in-America" grade and 956 men of science who are comparable so far as the age factor is concerned, with 14,000,000 males of the generality. Among the 14,000,000 males of the generality 17,000 are distinguished by having biographical accounts in "Who's Who in America." The average man of the group comparable with the men of science had, therefore, one chance in 823.5 to be included in that book. One thousand men of the generality had a little more than one and one fifth (1.214) of a man included.

How do the brothers of distinguished men of science fare? According to the data presented by the men themselves on number of living brothers and the number found to be distinguished by the writer, 1,000 brothers of distinguished men of science have 87.75 among them who are

distinguished as defined. The ratio of these two proportions, 1.214 and 87.75, is as 1 to 72.78. According to these figures, if two men, one a brother of a man of science and one a man of the generality, shake dice for distinction, the brother of the man of science would win nearly 75 times to one winning by the man of the generality.

How were these ratios obtained? Nine hundred and fifty-six men of science were found to have 106 brothers with biographical histories in "Who's Who in America" in Vol. 7, 1912–13 (Table V). This gives a ratio of 110.88 per thousand. Eight hundred and eighty-four men reported having 1,726 brothers, of whom 1,107 were living at the time of the report in 1910–11.

One thousand men of science would, therefore, have 1,263.6 brothers living at the time in question, of whom 110.88 or 87.75 per one thousand would be distinguished. The ratio of 17,000 in "Who's Who" to the comparable group of the generality, 14,000,000, being 1.214 per thousand, the brothers of men of science are, under the given conditions, 72.78 times as likely to become distinguished as the men of the generality.

There are factors tending to make this difference too small. Deaths of some of the brothers may have been omitted. Of this Cattell has said in his discussion on vital statistics:

> It is difficult to see how more valid statistics can be obtained than those supplied by scientific men, the order of birth, the dates of birth and death having been given; yet it is undoubtedly the case that all deaths are not recorded, especially for the brothers and sisters who died in infancy.[1]

A second factor is that of omissions in cases of distinguished brothers. Some few may have escaped notice in the search for those recorded in the particular volume used, but it is thought that there were few so omitted. It is true that the original reports failed to give anything like a complete account of the relatives who were known for their special performance in the various activities of life. A great many were reported who were not found recorded in any handbook and this is a feature that is of

[1] *Scientific Monthly*, October, 1917.

considerable importance, but it is a fact that but 84 brothers were given in the original reports who were found to be distinguished, while 146 were later found in one or more of the three handbooks used. Twenty-five of these were found to have become known during the course of the investigation, that is, included in editions of "Who's Who in America" for the first time after 1910–11. But if these factors were at work they tended to make the differences less than the figures indicate. The great difference as it stands, 1 to 72.78, is of sufficient validity to point to a resemblance between men of science and their brothers, and resemblance of the generality.

If we could know the number of brothers the men of the generality had and the number who became distinguished we could express the difference in resemblance of families of men of science and families of the generality. We do not know these facts, but the reader will see that the figures can not be far different from those given for the generality. The men of the generality would have approximately the same number of brothers per thousand as the men of science, and the 17,000 would be distributed among them in the same proportion as they are among the 14,000,000.

Fourteen millions may be a group unfairly large, that is, unfairly large as a number comparable to the thousand men of science. No better method than that used is known. The reader may make whatever selection of the general population he thinks best; he will find a difference that is highly significant, one that can not be explained as a matter of chance.

If 17,000 distinguished men of the generality came from a group of 14,000,000, the 106 brothers of men of science would, as a matter of chance, have had to come from a group of more than 84,000. What this means is that each man of science would have had to have about 80 brothers if the latter were no more likely than a man of the generality to become distinguished. If by some miracle towns and cities competed for honors determined by production of men of science, a country town of 7,000,

peopled by families of the grade of brothers of American men of science, would have to be handicapped by putting it with cities having a population of half a million if that competition were to be interesting.

RESEMBLANCE IN SCIENCE

What is the resemblance in performance in science? Table V gives the distribution of 106 brothers according to the direction of the work of the men whose brothers they are. It also gives the distribution according to two groupings, those whose work has been in science and those whose work has been in fields other than science. Some of those in the first group, the science group, have shown special performance in fields other than science, but none of those listed in the "non-scientific" group is known to have achieved distinction in science. It must also be noted that 28 brothers who have shown special performance in science are not included in this table. They are not included because they are not found in the particular handbook used in obtaining these ratios. Some of the 28 are in "American Men of Science," some are included in Appleton's Cyclopedia and some are in Who's Who of editions other than that used, namely, Vol. 7. The same holds true for biographies of 13 men whose work was not in science. The details of these facts may be seen at a glance in Table IV.

There were, as Table V shows, 47 distinguished in science and 59 who were not distinguished in science. Since there were approximately 2,500[2] or about one seventh of the 17,000 males in Vol. 7 who were workers in science, the chances of a man of the generality becoming distinguished, as defined, in that field is approximately one in 5,600.

It has been shown that 1,000 men of science would have about 1,300 brothers comparable, in age, with 14,000,000 of the generality. Since 956 men of science

[2] The biographies of the first 400 pages in Vol. 6 were gone over carefully and the number, per hundred pages, who had done work in science that would merit inclusion in such a book as "American Men of Science" was determined. The number in the remainder of the book was an estimate.

with x brothers had 47 brothers distinguished in science, 1,000 men of science with 1,263 brothers would have 49.2 so distinguished. If but one man in 5,600 of the generality achieves similar distinction, the brother of the man of science is 217 times as likely to become distinguished in science as a man of the generality.

Much might be said about the relative chances of distinguished financiers or industrial leaders and men of science having their biographies recorded in such a handbook as the one used in this investigation. It may be that men of science, being associated with public institutions such as schools, or large industrial laboratories, become known to the public and hence have their biographies recorded, although their performance no more merits it than, say, the high-priced manager of a department store. If such discrimination in favor of university people, especially men of science, exists, it should be determined. The facts are that so far as distinction goes there is family resemblance in the matter of achieving distinction, and that resemblance is greater in the direction of the specialized activity of science. The next section gives additional evidence of this specialized resemblance.

The Starred Group

There were 26 of the brothers who were members of the starred group. That is, 26 of the brothers of the men of science belong to the group itself. Three, however, were in the first edition only, leaving but 23 for comparisons with the groups under consideration. Since 23 of the x number of brothers of 956 men of science belonged to the starred group, 24 of the 1,263 brothers of 1,000 men of science would belong to the starred group. About two per hundred, or 20 per one thousand belong to the starred group, whereas 14,000,000 men of the generality have one for about 1,150 of their number. The brothers of men of science, therefore, have according to their numbers about 230 times as many of their

group belonging to the starred group as men of the generality.

There are in the starred group of relatives 58 relationships; 26 brothers, five fathers and five sons, one uncle, one nephew and 21 cousins. Only the brothers and cousins are comparable groups and the figures show that four fifths as many male cousins as brothers obtained positions in the starred group. There are, however, four times as many male cousins as brothers who have as a matter of chance the opportunity to obtain such a position. This evidence may be used as the reader sees fit. He may explain the difference in terms of nepotism or as congenital equipment which in turn may be explained by similarity in germ plasm which varies directly as the nearness of blood relationship. The figures show that a brother of a starred man is five times as likely to belong to the starred group as a male first cousin.

SISTERS

In Table IV will be found the distribution of the biographies of the 13 sisters who are known to be distinguished. All 13 are found in "Who's Who in America," but only 11 are recorded in Volume 7. By the use of the method employed in the selection of the 14,000,000 of the generality for comparison in the case of the brothers, there would be found approximately 13,000,000 females for a similar comparison for the women. Since the number of women in Volume 7 of "Who's Who" is approximately 1,700, the relation between the number of women who achieve distinction and the number who are of the same average age limits is found to be as one is 7,647, or .131 per thousand. Ten thousand adult women of the age limits assumed would, according to these figures, be represented by one and a third of their sex. Ten thousand men of the grade of our group would have, according to the figures above, 115 distinguished sisters. This seems to be a startling difference in spite of the small number of cases of sisters.

There were 884 records of men who reported the facts

concerning sisters living in 1910–11. They reported having 1,043 living at that time. If this number is correct, 1,000 men would have had, approximately, 1,180 sisters, of whom 11.5 would be distinguished. Since 11.5 in this number, or 9.28 per thousand were distinguished, in the same sense that .131 of the generality were distinguished, a sister of a starred man of science is 70.8 times as likely to achieve distinction as a woman of the generality.

It would be uncritical to make much of the close resemblance betwen the two values obtained in the matter of resemblance of men of science to their brothers and sisters. The fact that the number turns out to be approximately 70 in both cases is interesting and perhaps significant in spite of the small number of sisters found in the handbook used.

It is not known what per cent. of the women of distinction are workers in science but certainly not ten per cent. About five per cent. of the persons included in "American Men of Science" are women. Four, or over a third of the eleven of the sisters are known for their work in science. Here again, in spite of small numbers, the evidence of family resemblance is in the direction of specialized performance.

Fathers

There were 944 replies giving the necessary vital statistics of the fathers living in 1910–11. There were 246 reported living. There were 29 of these 246, or, 117.9 per thousand included in Volume 7 of "Who's Who in America." Eleven, or over one third, were distinguished in science. On first thought it might be supposed that this is evidence of a greater resemblance between men of science and their fathers than between themselves and brothers. This, of course, would be a difficult matter to explain in organic terms. The greater the number of years a man lives, the greater his opportunity, other things being equal, of obtaining a place in the ordinary biographical handbook. The chances of a person who dies at 20 are practically nil. Relative length of life may be the explanation.

MOTHERS

Three mothers of the 956 are known to be distinguished. This number, though small, is significant. The reader may be interested in turning to Table IV and noting the number of distinguished brothers and fathers of the mothers.

Social inheritance, such as family tradition, family wealth and occupation may direct the activities of an individual. It may be that families with university traditions have a very special advantage over the ordinary family in its chances for distinction. If this is so, more people should have the opportunity for university traditions.

SUMMARY

The investigation has shown: (1) That more than one man in four of the starred group of American Men of Science is related to one or more persons of distinction as defined; (2) that for one particular measure of distinction, the brothers of men of starred group are approximately 70 times as likely to become distinguished as a man of the generality; (3) that the resemblance is in the direction of the performance as well as the quality as shown by the number of brothers distinguished in science, being for the brothers 217 times that of the generality; (4) that the resemblance within the starred group gives additional evidence of specialization in similarity, being for brothers 230 times that of the generality and four times that of cousins; (5) that the data on the sisters closely approximate the figures on the brothers, though the number involved is small—the figures go to show that the sisters were approximately 70 times as likely to become distinguished as women of the generality; (6) that the direction of the performance was again favorable to science, being one third of the total, but that the small number concerned makes significance questionable; (7) that 29 of the 246 fathers or 117.9 per thousand of those living at the time of the investigation were men of distinction; (8) that three mothers were women of distinction.

(To be continued)

SHORTER ARTICLES AND DISCUSSION

LONGITUDINAL DIVISION OF THE TENTACLES OF HYDRA FUSCA

SINCE about the middle of the eighteenth century there have been frequent references to the occurrence of branched tentacles in Hydra. At least three naturalists of that period (Baker,[1] Rösel von Rosenhoff,[2] Trembley[3]) have left records of the observation of such abnormalities. Wetzel[4] observed branched tentacles on his experimentally treated animals and on at least one not so treated. He found in this last case that the phenomenon was due to the process of fusion of two neighboring tentacles. Rand[5] found several cases of fusion of tentacles during the course of his experiments with this animal. While carrying on similar experiments Parke[6] observed frequent cases of branched tentacles. Here, too, the branched appearance was due to a stage in fusion. Leiber[7] found a Hydra with two "heads." Each "head" bore, among other normal tentacles, one which was branched. Leiber thought, since the body was dividing, the tentacles must also be undergoing division. He could not be certain, however, because he neglected to count the tentacles at the beginning of his observations. Koelitz[8] observed forked tentacles and found the forks fusing into a single structure. Koch[9] found forked tentacles and regarded them as stages in fusion. Several investigators, among whom are Jennings,[10] Parke,[6] Leiber,[7] Korschelt[11] and Koelitz,[8] have reported cases of longitudinal division of the column of Hydra but so far as I have been able to determine, with the possible exception of Leiber, no one had witnessed such a process in the tentacles of this animal prior to the observations I desire to place on record at this time.

On December 2, 1918, while using some Hydras for class work obtained from Powers and Powers, Lincoln, Nebr., some weeks before, I had my attention called to two individuals each of which possessed one bifurcated tentacle among others of normal appearance. One of these animals was lost by the student who discovered it; the other was isolated and set aside for observation. At that time it was possessed of four normal tentacles in addition to the bifurcated one. Unfortunately, this ani-

mal was forgotten for four days. When examined it presented a most remarkable appearance. Altogether, there were fourteen tentacles present, but these were varied in position and form. Five were normal in appearance and position, five were normal in position but reduced in size, two were above the tentacle zone upon the hypostome and reduced in size, and the remaining two were below the tentacle zone and somewhat reduced in size. A bud attached to the parent possessed four normal tentacles and a very short one, all in the usual position. Further observations were cut short by the death of the animal before any further significant changes took place. From subsequent observations, however, I think there is little doubt that the increase in the number of tentacles occurred as a result of longitudinal division.

A thorough examination of all my cultures was then made with the hope of discovering more animals in this interesting condition. No more were found until December 30. I then found one animal which possessed two normal tentacles, two attached at the distal ends and one which was bifurcated near the distal end. This Hydra did not long survive and died unchanged.

The following day an individual was found which not only showed the desired characteristics but which was also in a fairly vigorous condition and lived long enough for me to make certain very interesting observations on the course of division of the tentacles. When discovered this animal had eleven tentacles of three sorts. Six of these were normal, two were reduced in size and insecurely attached to the body and three were bifurcated at different distances from the base. Frequent observations were made on the animal during the next few days. During this time three tentacles completely divided and one other partially so, leaving no doubt as to the general method involved. The plane of division was usually parallel to the antero-posterior axis of the body but in one case the plane of division was at right angles to this with the result that at the completion of the process one of the new tentacles was displaced some distance upon the hypostome. This displacement was probably made more pronounced by cell movement and rearrangement in that region. In one other instance before a tentacle had quite completed division one of the new appendages thus produced began another division, but the second

branch persisted for only a short time and then was pinched off and disappeared. No cases of fusion of the tentacle were found at any time. In addition, however, to the process of division of the tentacles this animal also showed a remarkably rapid resorption of these appendages. Indeed, at the end of the period of observation, in spite of the rapid division, so much resorption took place that there remained but six tentacles all apparently normal.

On January 10, 1919, another animal was found showing something of the same peculiar division process. This Hydra possessed three normal tentacles and two more joined at the distal ends. These, I should say, must have arisen from the division of one for the process went on until the two were nearly separated when they broke apart, leaving a portion of one attached to the other. Of course in this case the division did not start at the distal end as usual but somewhere below after which it proceeded distally or possibly in both directions.

Although I have repeatedly searched through my cultures during the past three years no animals showing the peculiarities described in this paper have since been found, with one exception only. This one Hydra was found in March of the present year and showed about the same condition as the animal last described above. I was not able to study the animal and so, of course, I am unable to state whether in this case the split tentacles arose as a result of fusion or actual division.

It has been suggested by Koch[9] Frischholtz[12] and others that overfeeding and sudden changes in temperature may cause resorption of tentacles, and longitudinal division of the body of Hydra. My animals were kept in a fairly constant temperature and fed frequently but not richly upon Cyclops and other small crustacea. So far as I know there were no particularly abnormal conditions.

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MICROSCOPICAL METHODS USED IN EXAMINING CHROMOSOMES IN IRON–ACETOCARMINE

FOR nearly three years I have been counting and observing the chromosomes in pollen-mother-cells and pollengrains of Datura,[4] Canna,[3] and other flowering plants, after fixing and staining with iron-acetocarmine.[2] During this time it has been found advantageous to adopt those particular microscopical methods which successive experiments showed to be best fitted for the observation of chromosomal structure in a fluid differing little from water in its refractive index.

Miss N. M. Stevens[10] and others who have extensively used the acetocarmine method for the examination of animal chromosomes seem to have employed oil-immersion objectives, with or without an oil-immersed aplanatic condenser. Excellent work

* These papers were not available for reading. I have quoted from other authors.

has been, and can still be, done in this way. However, if the same microscopical methods are employed for observing chromosomes in diluted acetic acid of refractive index about 1.35, as for objects in xylol-Canada balsam with a refractive index of say 1.52, then it seems that the full possibilities of the iron-acetocarmine method will not be reached. In the first case the contrast between the chromosome and the medium is one both of color and refractive index, in the second case the contrast is almost wholly one of color.

The usual theoretical view is that the resolution, and hence the useful magnification, depends, other circumstances being similar, on the working aperture; that is, half the sum of the utilized aperture of the condenser and the whole aperture of the objective. This seems to have stood the test of experiment.[6] Hence to increase useful magnification, with chromosomes in 45 per cent. acetic acid, and with an oil-immersion objective and condenser, the condenser would naturally be connected with the slide by immersion oil or by water. The former method has only a slight advantage here, and experience shows it cannot conveniently be used where large numbers of slides are daily examined, because of the time spent in cleaning slides, stage, and condenser from immersion oil. With either an oil-immersion or a water-immersion objective, used on objects in water or fluid of similar refractive index, water can, without any marked loss, be used instead of oil to connect the condenser with the slide, and the drying of the condenser and slide with blotting-paper requires but little time. If the slide is too thin, a blank slide of the right thickness is put under it, and connected with it by distilled water.

When an aplanatic condenser of high aperture is focussed, an image of the source of light (flame, white cloud, doubly ground glass, etc.) is, of course, formed in the exact plane of the object. So much of this image as fills the field of view of the eyepiece is utilized, but the outlying unutilized parts often cause a slight fog over the image of the object. If all or most of these outlying parts are cut off by a diaphragm (close to the ground glass or flame) I find, as others have found, that the image of the object is usually sharpened,[1] the utilized aperture of the condenser being unchanged.

With the ordinary plane mirror of the microscope, with an angle of incidence of about 45 degrees, there are usually two

fairly bright images of the source of light besides the one primarily reflected from the silver. These two extra images partly neutralize the advantages of the employment of an achromatic or aplanatic condenser. They can be removed, with marked gain, by using a right-angled reflecting prism,[8] which I find about as easy to manipulate as the ordinary plane mirror. If it is fixed on the blackened surface of the plane mirror one hardly notices the change, except by the increased light in the single image. This prism need be no wider than the lowest lens of the condenser.

A yellow-green light filter, used between the ground glass of the lamp and the mirror or reflecting prism, has the following well-known advantages.[9] (*a*) Transmitting mainly the color for which ordinary achromatic objectives are corrected, its use makes them nearly equal to apochromatics. (*b*) Those with experience of it will I believe mostly agree that the yellow green is more grateful to the eyes, especially if microscopical work occupies several hours daily all the year. (*c*) The yellow-green screens being partly or wholly opaque to red light, the carmine-stained chromosomes will be dark or black, and markedly sharper in outline, even with apochromatic objectives. (*d*) If the yellow green has a higher average wave frequency than the artificial light used, then resolution is increased. (*e*) The use of several grades of green screen of different depths of color will serve to increase or decrease the intensity of the transmitted light, while the most suitable aperture in the condenser is retained unaltered. I find the following series of the Wratten gelatine films[7] a useful one (and it includes the three which Spitta[9] found best); namely numbers, 66, 56, 57A, 58, and 61. These transmit respectively, 58, 48, 34, 23, and 18 per cent. of the incident light.[11] (Number 66 is usually somewhat too light for the Mazda C lamp, and number 61 may require the arc.) These films are mounted with balsam between two pieces of parallel-plane glass.

After using the monocular microscope nearly every working day for two years, and the binocular eyepiece for nearly a year, I consider that the gain in easy visibility resulting from the employment of both eyes more than counterbalances any slight defects of the binocular. The binocular image is more vivid, as Jentzsch[5] stated, despite the double reflections and the thickness of glass traversed by the light, than the one-eye image

of the old pattern. The tube-length of the binocular may be increased, when necessary, by fitting detachable collars of appropriate depth to the eyepieces.

The oil-immersion objective, achromatic or apochromatic, has been calculated and constructed by the makers primarily for the observation of objects in Canada balsam, or in media of similar refractive index. Therefore if a stratum, one or more hundredths of a millimeter thick, of water, or of a fluid approximating water in refractive index, such as 45 per cent. acetic acid, lies between the coverglass and the object of an oil-immersion objective, the definition is more or less impaired by spherical and chromatic aberrations. As is well known, the spherical aberration can be partially compensated by sufficiently increasing the tube-length of the microscope. It is also a familiar fact that good definition can be obtained under these circumstances if the object is in close contact with the coverglass. But a water-immersion objective, with an aperture of 1.20 or 1.25, only requires correcting by setting the graduated collar to the thickness of the particular coverglass in use, and may then, of course, be focussed down for several hundredths of a millimeter through a liquid of refractive index approximating 1.33, without a perceptible loss of definition. The measurement of coverglass thickness takes only a few seconds, and consists in screwing down the graduated fine adjustment from the upper to the lower surface of the coverglass, and taking the required thickness from a previously prepared table. In checking such a table the Abbe test plate is useful. I find it quicker and more accurate to measure the coverglasses than to set the collar by trial of the best definition. If water-immersion objectives without correction collars are used, of course coverglasses of approximately 0.17 mm. must be selected, and the slight final adjustments are made by increasing or decreasing the tube-length.

In the daily routine of searching over many preparations of chromosomes under large coverglasses, two objectives at least are necessary; a finder, and an immersion lens of the highest attainable aperture. If an oil immersion is used, everyone has had the experience that the definition of the finder is annoyingly marred by the traces of oil on the coverglass; whereas with a water immersion an occasional application of blotting-paper keeps the cover dry and clean. Thus the high-apertured

oil-immersion objective is used mainly for the close study of specially selected chromosome groups, which are in contact, or nearly in contact, with the coverglass.

Summary.—In the microscopical examination of chromosomes in 45 per cent. acetic acid, it was found more convenient to connect the condenser with the slide by water than by oil; it was usually of advantage to use a diaphragm on the source of light, and when this was done the employment of a reflecting prism was naturally indicated; the green light screens advocated by Spitta were found of quite considerable benefit; the binocular eyepiece was found to add greatly to the vividness and clearness of the image; while the contingent advantages of using a water-immersion objective were considered to repay the trouble of measuring all coverglasses.

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